

Chapter 16 The Caribbean Lowland Evergreen Moist and Wet Forests

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Introduction

The saying “geography is destiny” has been used by historians and economists to explain large-scale phenomena such as human trading routes, migration patterns, technological innovation, spread of disease, and the motivation for and outcomes of wars. In the context of Costa Rican ecosystems, one might also invoke the expression to frame more than five million years of the history of Costa Rica’s Caribbean lowlands. We do not imply that events have been or will be predictable, but rather that geography has played a critical role in Costa Rica’s Caribbean lowlands with respect to initial origin of the landmass, climate, patterns of vegetation, sites of early human settlement, colonial expansion, the construction of access roads, colonial and postcolonial exploitation of natural resources, conservation efforts, and current political and environmental issues. In this chapter we offer a brief overview of these topics, encapsulate major biological research efforts in the Caribbean lowlands over the past 50 years, and look into the future—always within the framework of geography at different scales.

Today the Caribbean lowland portion of Costa Rica, broadly defined, includes the entire Province of Limón (with its Caribbean Sea margin), plus portions of the Provinces of Heredia, Alajuela, and Guanacaste (with their northern edges along the Río San Juan and other stretches of Costa

Rica’s border with Nicaragua) (Fig. 16.1). For this map, we define the upper altitudinal limit of the area as 300 m, although some sections of this chapter will use slightly different elevations, depending on the standards of a particular

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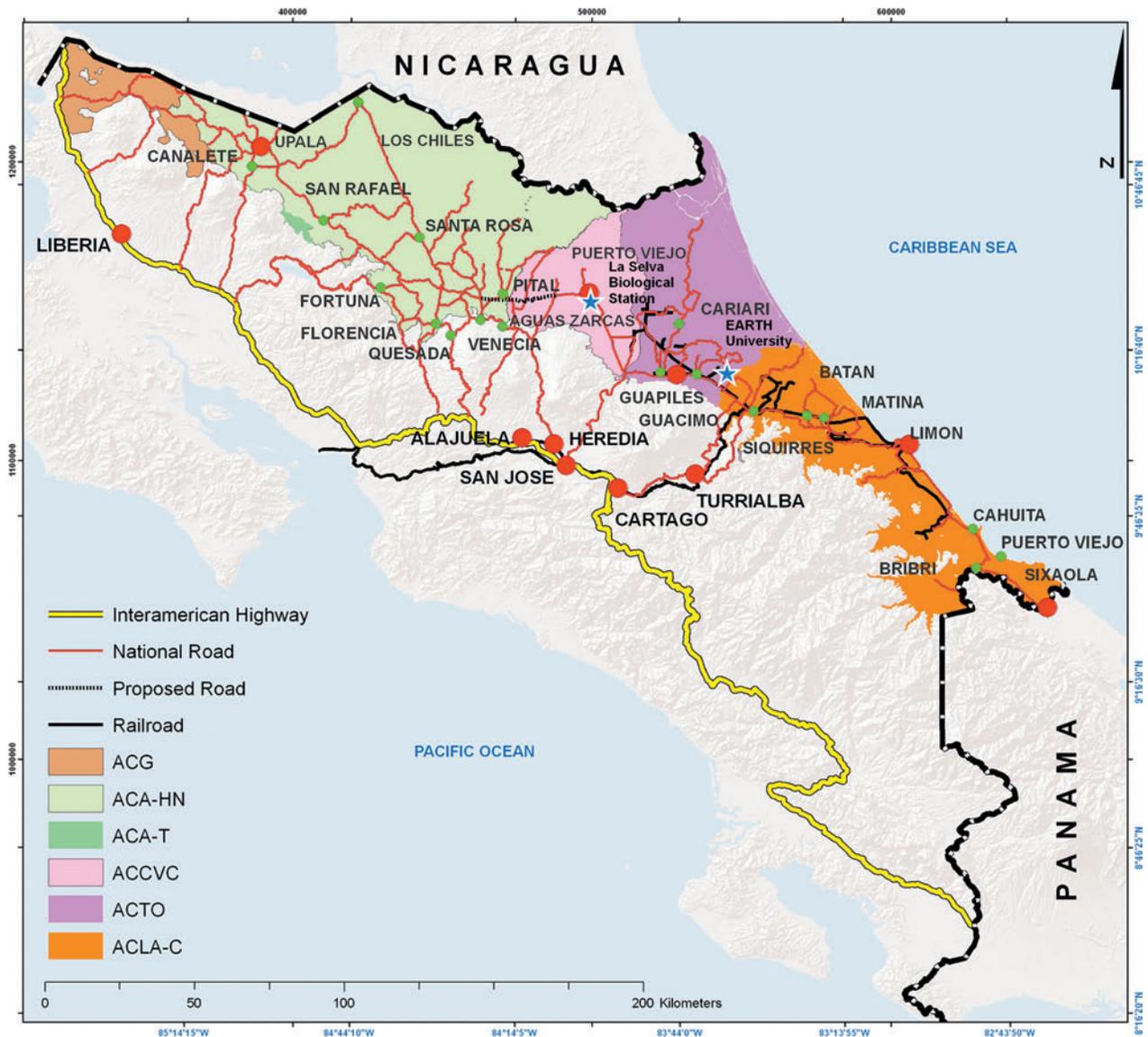


Fig. 16.1 Map of Costa Rica showing major roads, national population centers, as well as details of the Caribbean lowlands (shown in colors). The Pan-American Highway is shown as a thick yellow line. The northern edge of the zone is the border with Nicaragua (including the Río San Juan) and the eastern edge is the Caribbean Sea. Although the railway is no longer in use, its extent (solid black lines) is depicted here to illustrate the route taken by highland coffee from the Central Plateau to the port city of Limón during the late nineteenth and early twentieth centuries. Note that there are two towns labeled Puerto Viejo. One is in the canton of Sarapiquí (near La Selva Biological Station) and the other is near Limón. Unwary researchers heading to La Selva have been known to catch the wrong bus in San José and to end up on the Caribbean coast. The Caribbean lowlands have contributions from six of the country's 11 conservation areas. ACG (Guanacaste), ACA-HN (Arenal-Huertar Norte), ACA-T (Arenal-Tilarán), ACCVC (Cordillera Volcánica Central), ACTO (Tortuguero), and ACLA-C (La Amistad-Caribe). The La Selva Biological Station and EARTH University are indicated by stars.

field of study. At the northern end of the zone, we chose the watershed of the Río Sapoa as the boundary. This river drains into Lake Nicaragua, whereas all the rivers to the north and west drain into the Pacific Ocean. A more readily identifiable border is the northern stretch of the Panamerican Highway, which is virtually congruent with the Sapoa watershed boundary.

The Caribbean lowlands cover approximately 13,760 km²

or about 27% of the terrestrial landmass of Costa Rica. The major population center of this area is the port city of Limón, Costa Rica's second largest city, with a population of about 63,000 people. Other locations that receive frequent mention throughout this chapter include the OTS-administered La Selva Biological Station and EARTH University (Escuela de la Agricultura de la Región Tropical Húmeda). Six of the country's 11 conservation areas are represented in the

Caribbean lowlands, although three of them have only a small area represented in the lowlands. Fig. 16.2 shows the distribution of protected areas and indigenous reserves in the Caribbean evergreen, forested lowlands.

Historical Overview

We treat the history of the Costa Rican Caribbean lowlands in five sections:

1. Early tectonic activity (70 million years ago [mya]) through the Miocene shoaling of the Central American Seaway (CAS) and incipient closure of the Isthmus (from approximately 24 mya to 5.3 mya) but see Bacon et al. (2015)
2. Post-Miocene development and closure of the Isthmus until human arrival (from approximately 5.3 mya to 16,000 years before present [ybp])
3. Early human (indigenous) settlement until the arrival of the first Europeans (from 16,000 ybp to 1502 AD)
4. Colonial and postcolonial trends (from 1502 to the 1960s)
5. Recent history (from the 1960s on)

The major topics considered for all of these time segments have been radically rethought in the past 25 years. New sites (geological, paleontological, archaeological, and ecological), new techniques (high-resolution remote sensing, climate modeling, dated molecular phylogenies, in addition to analysis of isotopes, phytoliths, and starch grains), and new paradigms (origins of tropical agriculture, demographic collapse, the pristine myth) have all influenced current thinking. We cannot offer definitive answers to many of the most engaging questions or even cover the complexities of the debates. Additionally, we are only too aware that our treatment now will seem woefully out of date in a few years. We do hope that our presentation here will capture some of the excitement and fullness of ongoing work, guide the reader to unexpected sources of information, and perhaps even prompt new lines of investigation.

Early Tectonic Activity through the Miocene–Pliocene Closure of the Isthmus

Today the Caribbean Sea waters of Costa Rica and Panama are warmer (Lessios 2008), saltier (Benway and Mix 2004, Haug et al. 2001, Keigwin 1982), and less productive (Cannariato and Ravelo 1997, Jain and Collins 2007) than are the Pacific coastal waters. These differences have accumulated (but fluctuated) for the past many millions of years, as the wide abyssal Central American Seaway (CAS)

between the oceans underwent a series of shoaling events throughout the Miocene and into the Pliocene. The primary engine for these changes has been tectonic activity for more than the past 70 my in one of the world's most complex intersections of oceanic and continental plates (Alvarado et al. 2009, Van Avendonk et al. 2011, Buchs et al. 2010, Hoernle et al. 2002, Hoernle et al. 2008, Sadofsky et al. 2009, Wegner et al. 2011, Werner et al. 1999).

The Caribbean seafloor (Caribbean Large Igneous Province or CLIP) is generally (but not universally) acknowledged to be of Pacific origin and to have shoved its way through the gap between North and South America about 65 mya. The Farallón Plate fractured 23 mya (Lonsdale 2005), at which time the resultant Cocos Plate portion began subducting beneath the Caribbean Plate along the Middle American Trench (MAT), which is a stretch of Pacific coast from Mexico to Panama. This subduction caused the lifting of the seafloor and the volcanic activity that created the Costa Rican and Panamanian portions of the isthmian land bridge between North and South America (Sak et al. 2009). The convergence rate of the Cocos and Caribbean plates has fluctuated over the millennia and is currently about 90 mm/year offshore of Costa Rica (Harris et al. 2010, Hoernle et al. 2008). The thickened but buoyant section of the Cocos Plate identified as the Cocos Ridge is positioned off the Osa Peninsula in southern Costa Rica (Hoernle et al. 2002).

The Talamanca Mountains represent the arc highlands and the Caribbean coast area around Limón is the back-arc basin of this ridge (MacMillan et al. 2004). The failure of smooth subduction of this ridge has been implicated by some geologists as the cause of the highly destructive 1991 Limón/Cahuita earthquake on the Caribbean side of Costa Rica (Fernández-Arce 2009; Cortés, chapter 17 of this volume), but other authors consider that the slab subducting beneath the Talamanca Mountains is behaving “normally” and that the buoyant Cocos Ridge piece is only beginning to enter the MAT 50 km offshore from the Osa Peninsula (Dzierma et al. 2011).

The periodic upheavals in and final cessation of the deep water CAS, along with the formation of the Caribbean shores of Costa Rica and Panama, deflected the Atlantic waters northward along the east coast of North America. By mechanisms still not definitively elucidated, the establishment of the Isthmus is thought by many scientists to have created the Gulf Stream and to have initiated the series of Pleistocene Ice Ages (Bartoli et al. 2005, Haug et al. 2004, Nof and Van Gorder 2003, Steph et al. 2006—but see Molnar 2008 for other perspectives), from the last of which the world emerged about 10,000 years ago. From this deep historical perspective, therefore, the Caribbean

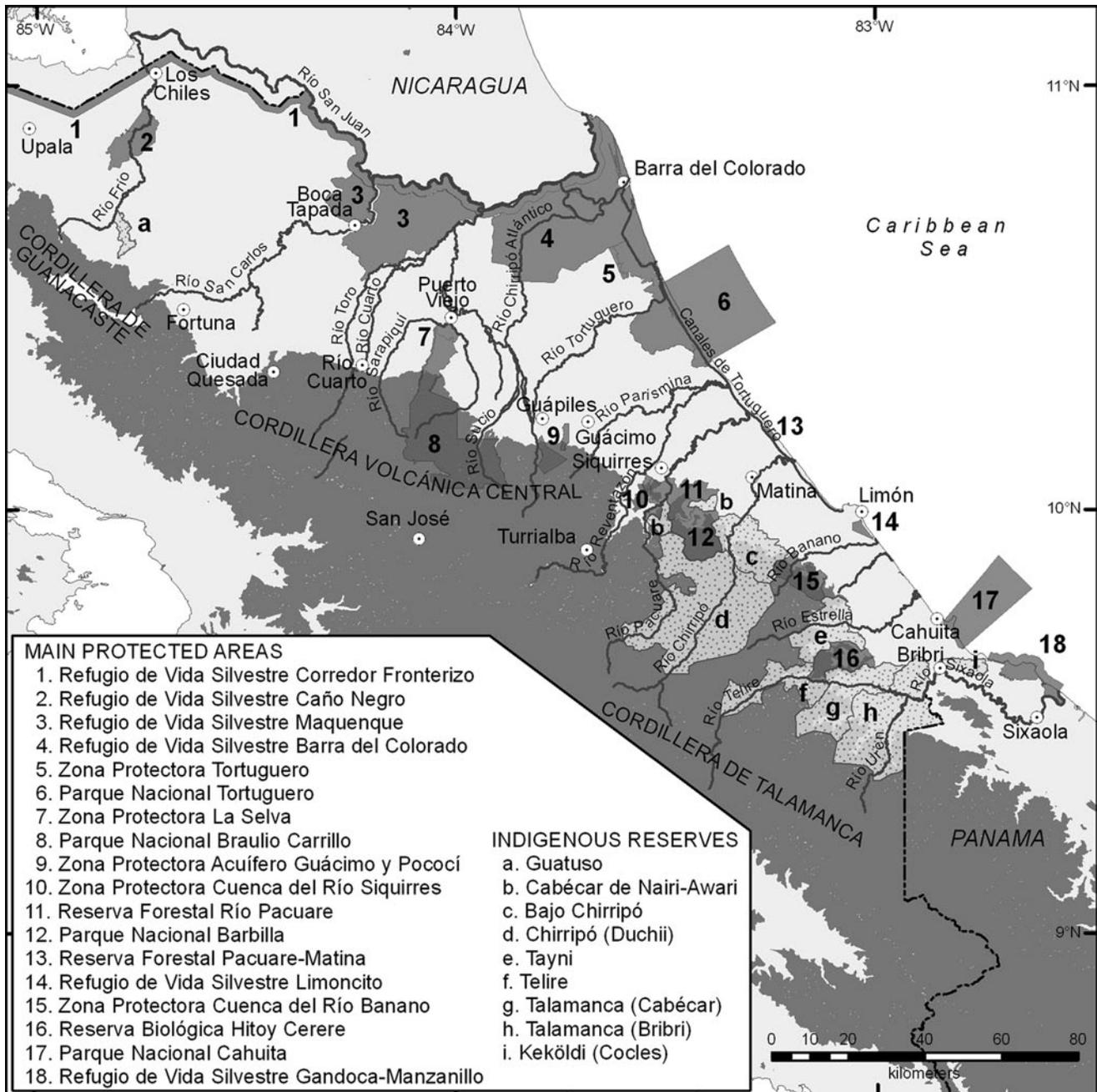


Fig. 16.2 Map of the main protected areas and indigenous reserves found in Costa Rica's Caribbean evergreen moist and wet forest lowlands. Map prepared by Marco V. Castro.

lowlands of Costa Rica can be assigned a major role in “the most important natural event to affect the surface of the earth in the past 60 million years” (Coates 1997).

The Miocene Epoch was a 20-million-year stretch of time (between about 25 and 5 mya) during which the space now occupied by Panama and Costa Rica was transformed from an open seaway to an island arc (or peninsula) and finally

to a continuous isthmus. The climate fluctuated, from cool Early Miocene to the Middle Miocene Climatic Optimum 12–15 mya and through a few more warming and cooling cycles after that (Kürschner et al. 2008, You et al. 1996). Maximum temperatures at 12 mya are usually described as about 5 degrees C warmer than they are now in the lowland tropics. The bits of basalt and limestone that were being

pushed above sea level in the area that is now Caribbean-side Costa Rica immediately became potential colonization sites for all manner of terrestrial organisms waiting in the wings (North and South America) and in the winds.

Our knowledge of plant communities in the New World lowland tropics of the Miocene has been and continues to be fragmentary. Good fossil sites are rare and widely scattered in space and time. The current lowland tropical vegetation of Mexico and Central America was previously considered to be primarily of South American origin (Gentry 1982, Hammel and Zamora 1993, Wendt 1993). Ancient transatlantic dispersal (in both directions) had been postulated for fern spores, based on the closest living relatives of some fern genera being found in Africa and South America (Moran and Smith 2001), but this mechanism was invoked for few angiosperms. North and South American floras shared only 2.6% of their palynomorphs (fossil pollen morphotypes) in the Middle Eocene (45 mya), but shared 30% after establishment of the Isthmus (Burnham and Graham 1999).

These data were previously taken as evidence of isolation of North and South American floras before the land bridge connection, followed by plant dispersal across the land bridge, with a south to north flow predominating. The fossil palynomorphs from a late Miocene site near Limón, Costa Rica, led to a reconstruction of the site as a moist, warm, closed-canopy forest (with an abundance of ferns and lycophytes in the understory) bordered by a *Rhizophora* mangrove swamp—no palms, no grasses, and no evidence of savanna-like habitat (Graham 1987, 1992, Graham and Dilcher 1998). The heights of the exposed land formations near Limón were estimated to be about 1,400 m in the early Miocene and 1,700 m in the late Miocene—this low relief would also imply that there was not yet a distinction between vegetation assemblages on the two sides of the Isthmus (Graham and Dilcher 1998). During the Miocene there was probably greater divergence in marine organisms than in the terrestrial vegetation on the Pacific and Caribbean sides.

Two new techniques are expanding and changing our image of the evolution of New World tropical vegetation. The proliferation of dated molecular phylogenies of plant groups and the study of phytoliths—small slivers of silica (“plant opal”) in plant tissues that are diagnostic to the family, genus, or even species level—are providing higher resolution and recalibrated dates for the evolution of tropical plant communities. Recent molecular biogeographic studies of several plant groups suggest multiple instances of long-distance dispersal between Africa and South America (Lavin et al. 2004, Pennington et al. 2006, Renner 2004a, b, 2005) and across the Central American Seaway before isth-

mian closure (Cody et al. 2010). These techniques could greatly enhance and modify our understanding of the early colonization and subsequent evolution of the Caribbean lowland vegetation (Pennington et al. 2006).

An intriguing but little explored potential source of inorganic material and life forms for the emerging isthmus would have been transoceanic winds. Much has been made in recent years of the enormous African dust clouds (from the Sahara and Sahel deserts) that are affecting the Amazon Basin (Ansmann et al. 2009, Bristow et al. 2010, Kallos et al. 2006), contributing mineral elements to Jamaica and Barbados (Caquineau et al. 2002, Muhs and Budahn 2009), spreading crop diseases (Brown and Hovmøller 2002), possibly contributing to Caribbean coral diseases (Garrison et al. 2003), threatening human health (Griffin 2007, Mundt et al. 2009), and probably modifying global climate (Perkins 2001, Washington et al. 2009). Dust fluxes across the tropical Pacific have been less well documented (McGee et al. 2007) and the deep history of all of these winds remains largely unknown. It is reasonable to imagine dust, pollen, spores, and pathogens travelling on these winds, but apparently larger organisms can be borne along as well. A well-documented, wind-assisted locust plague in 1988 brought a swarm of these insects 5,000 km across the Atlantic from Western Africa to the Caribbean in four or five days (Lorenz 2009).

In summary, the scenario for the Miocene island arc phase of the Caribbean lowlands involves the following factors: overall increase in land area caused by seafloor lifting and volcanism (modified by fluctuations in sea level), warm temperatures peaking at 12 mya, and colonization of land by plants (probably dominated by southern forms), mammals (dominated by northern forms), and birds (both northern and southern contributions). For other taxa, a dated molecular phylogeny strongly suggests that the turtle *Rhinoclemmys* (the only New World genus of the family Geoemydidae) crossed to the New World via Beringia during the Eocene, and then into South America during the Miocene before land bridge closure (Le and McCord 2008). A similar hypothesis has been promoted for the New World *Polyommatus* butterflies (the “blues” of the family Lycaenidae) having moved across Beringia from Asia and then into South America about 10.7 mya (Vila et al. 2011). South American taxa thought to have arrived in Central America before the completion of the isthmus include túngara frogs (Weigt et al. 2005), certain vipers (Zamudio and Greene 1997), and ctenosaur lizards (Hasbún et al. 2005). The pygmy rain frog (*Pristimantis*) appeared to have radiated from the Pacific side of Costa Rica and Panama over to the Caribbean side during the Miocene (Wang et al. 2008).

Abiotic and biotic inputs from Africa remain a tantalizing but largely unsubstantiated possibility.

Closure of the Isthmus until Human Arrival

The closure of the Isthmus is associated with the image of a connecting bridge over which plants and animals could freely make their way. A postulated change in the corridor vegetation from a mesic rainforest to an open savanna or to a patchwork of habitats during the first million years after closure would have affected the movements of some groups of animals (Webb 1991, Woodburne et al. 2006, Woodburne 2010). For decades the Great American Biotic Interchange (GABI) was heavily biased towards consideration of mammals, with some embarrassingly chauvinistic statements about northern hardiness or competitive superiority to explain the dominance of north to south flow, both in terms of newly arrived colonists and persistence of lineages to the present day. Carnivores, camels, horses, rhinos, gomphotheres, and rabbits (34 genera in total) moved south (see Alvarado and Cárdenes, chapter 3 of this volume). Ground sloths, armadillos, opossums, and some archaic ungulates moved north (17 genera in total) (Woodburne 2010, Woodburne et al. 2006). Each group of migrants left off representatives in Costa Rica, Panama, and the rest of Central America. Today the mammalian faunas of this slender landmass continue to be a mixture of northern and southern forms (Timm 1994). The rodents and New World primates present their own special problems in biogeographic reconstruction (MacFadden 2006, Poux et al. 2006, Reguero et al. 2007, Schrago 2007). Most attempts to reconstruct the early colonization of the land bridge between North and South America for most plant and animal groups have been made at a larger spatial scale and not for Caribbean lowland forms specifically.

One particular example of a Caribbean lowland fossil plant assemblage deserves special attention. A series of Pleistocene plant macrofossil sites preserved under clay-rich volcanic deposits along the Río Puerto Viejo near the La Selva Biological Station reveals interesting patterns. The exact dates of these deposits have been difficult to establish, but they seem to be at least 46,000 years old. Most taxa identified from the fossil leaves, fruits, seeds, wood, pollen, and spores represent taxa present in today's forest, but some macrofossils and pollen represent taxa that are now found only at higher elevations (Horn et al. 2003). Pollen can easily find its way downslope, but the presence of macrofossils of more cool-adapted plants, along with the absence of *Pentaclethra* pollen, is strong evidence that the climate at the La Selva Biological Station might have been 3 degrees C cooler at this time during the Pleistocene than it is now.

Early Human (Indigenous) Settlement until Arrival of Europeans

At least five topics that have generated considerable heat and light in recent years concern humans in the New World. When did humans arrive in Central America? What impact did indigenous people have on New World habitats? What impact did contact with Europeans have on the indigenous human populations? Have episodes of demographic collapse of human populations led to climate change through the intermediary of forest regeneration and carbon sequestration? How will humans interact with and influence their tropical environments in the future? These questions are explored in the context of the Caribbean lowlands of Costa Rica after a brief review of the peopling of Central America.

Humans arrived in the New World via the Bering Land Bridge some 16,000–23,000 years ago, towards the end of the last glacial period. Evidence from mitochondrial DNA haplotypes indicates that a relatively small founder population of approximately 5,000 individuals (Goebel et al. 2008) may have had a “standstill phase” in Beringia and then moved rapidly along the deglaciated Pacific coast (with the aid of boats) into Central and South America (Fagundes et al. 2008, Fix 2002, Tamm et al. 2007), reaching the tip of South America in about 1,000 years.

For years, the general view has been that these Amerind groups left a small and shallow footprint on the landscape. The “ecological Indians” lived in harmony with the environment and did not overexploit resources or cause large changes in the ecosystem, either because of their practices or their small populations (Krech 1999). That stereotype was challenged with the proposal by Martin (1967, 1984) that the extinction of most of the mammalian megafauna of the New World at the end of the Pleistocene (about 10,000 years ago) was caused by human overhunting. However, the basic idea still persisted through the 1980s and into the 1990s that the rainforests of the Amazon and even of Costa Rica were virgin (or “undisturbed”) forests with only scattered evidence of previous human habitation (see reviews of aspects of this topic in Clark 1996, Clement and Junqueira 2010, Denevan 1976, 1992, Heckenberger et al. 2003, Willis et al. 2004). In contrast, recent evidence from archaeological sites, lake sediment deposits, and the reconstruction of plant communities presents a very different view—one in which large populations of indigenous people had a deep and broad impact on the landscape throughout Central and South America (Arford and Horn 2004, Bayón et al. 2011, Iriarte and Alonso 2009, Iriarte et al. 2004, Lane et al. 2008, Mann 2005, Stahl 2004).

The current indigenous people of Costa Rica's Caribbean lowlands belong to the Chibchan language group.

The Chibchan-speaking people probably separated from other groups between 6,000 years ago (Ruiz-Narváez et al. 2005) and 8,000–10,000 years ago (Torroni et al. 1994). This language group includes the modern day Bribri, Cabécar, Guaymí (Ngöbe), Boruca, Teribe, Maléku, and Kuna of Costa Rica and Panama, in addition to various tribes in northern South America. This group does not include the Embera and Wounaan of Panama (living languages in the Chocó language family) or the Nicoya Peninsula-based Chorotega (an extinct language in the Oto-Manguean language family). Costa Rica's indigenous people now constitute a small percentage (1–2%) of the total population of the country but their numbers at the time of European contact are estimated to have been around 400,000 (Molina and Palmer 2007), with a major center in the Nicoya Peninsula and several others located in other parts of what is now Costa Rica.

The human genetic evidence is congruent with the language grouping of the Chibchan-speaking people. Data from mitochondrial DNA (Keyeux et al. 2002), Y chromosome (Ascunce et al. 2008, Ruiz-Narváez et al. 2005), X chromosome (Bourgeois et al. 2009), and gammaglobulin allotype (Callegari-Jacques et al. 1993) studies of living people and archaeological remains all support the coherence of this assemblage as distinct from other Amerind groups. Interestingly, within the Chibchan-speaking peoples there seems to have been little intermarrying among the tribes over the past several thousand years, even between neighboring communities such as the Bribri and Cabécar (Ruiz-Narváez et al. 2005) or with non-indigenous people (Ascunce et al. 2008).

Between 14,000 and 10,000 years ago the climate in Central America was cooler and drier than it is now and the vegetation was probably at least partially thorn-scrub (Burnham and Graham 1999). There was an abundance of mammalian megafauna (ground sloths, mastodonts) as well as many now-extinct mammals of medium to large size. About 10,000 ybp the climate in the current Neotropical latitudes changed rapidly, becoming warmer and moister, with related changes in land cover (Hughen et al. 2004). A concomitant and rapid loss of mammalian megafauna (at least ten genera) and medium to large mammals (more than 35 genera), occurred from overhunting, climate change, disease, or some combination of these factors (Barnosky et al. 2004, Brook and Bowman 2004, Burney and Flannery 2005, Dillehay 2009, Doughty et al. 2010, Johnson 2002, Lyons et al. 2004, Martin 1967, Surovell et al. 2005), or from as yet undetermined causes (Stuart et al. 2004).

Whatever the timing and causation of events, the people living in Central America 10,000 ya would have been faced with dwindling populations of large mammalian prey items.

Piperno and colleagues have evaluated the food situation at this Pleistocene–Holocene transition in Central America by using optimal foraging theory and a niche breadth model (Piperno and Pearsall 1998), in addition to the study of phytoliths and the new technique of starch grain analysis. With the loss of high-return items (large mammals), human diets would have diversified, initially probably incorporating more starch-filled tubers. In Panama, 8,000 years ago, people were growing and processing corn (maize, a crop originally from Mexico) and manioc (cassava) (originally from Brazil), in addition to yams and beans (Piperno and Holst 1998, Piperno et al. 2000). In Peru, 8,000 years ago, people were eating domesticated varieties of squash and peanuts (Piperno and Dillehay 2008). Crop dispersal occurred apparently more often via exchange of plant germplasm rather than by movements of people (Dickau et al. 2007). Piperno specifically disputes colleagues who claim that these humans avoided the forest because of lack of food or the presence of diseases—of 22 Central American sites from around 10,000 years ago, nine are in some type of forest (Piperno and Pearsall 1998).

Evidence of occupation by indigenous people as far back as 3,000 years exists for the land that is now covered by the La Selva Biological Station. These forests were described in early ecological publications as pristine (Frankie et al. 1974, Hartshorn 1983). However, pottery and stone artifacts indicate that people lived in groups along alluvial terraces at La Selva 3,000 years ago (Sol Castillo 2000). On the basis of pollen records, it is also clear that there was corn cultivation in the Cantarrana Swamp 1,000 years ago (Kennedy and Horn 1997, 2008) and in other La Selva sites as far back as 2,700 years ago (Horn 2006, Horn and Kennedy 2001). The current distribution patterns of two species of palm trees also suggest landscape modification by humans at least a hundred years ago, before biologists and agroforesters had arrived on the scene (Clark et al. 1995). As an aside, a continuous record of *Pentaclethra* pollen at La Selva for the last 3,200 years (Kennedy and Horn 2008) demonstrates that this dominant tree has been well established for at least this length of time and is not a recent arrival. Charcoal deposits may be due to human-set or natural fires (Horn and Sanford 1992, Kennedy and Horn 2008).

The archaeological study of starch grains to infer indigenous diet and early agricultural development has not progressed at the sites of the Costa Rican Caribbean lowlands to the same extent that it has in Mexico, Panama, and Peru. However, the investigation of the species in cultivation in modern-day indigenous homegardens provides valuable insight into the historical record and also demonstrates the potential of homegarden plants to preserve the genetic diversity of agricultural crops (see chapters in Kumar and Nair 2010).

The Reserva Talamanca, a 54,000 ha lowland parcel between Puerto Limón and the Cordillera de Talamanca, has been the territory of the Bribri and Cabécar indigenous groups for several hundred years (Borge and Castillo 1997) and is currently the home to approximately 8,000 of the remaining 21,000 members of these groups. In 83 homegardens, 46 cultivated plant species were growing, including native species (*Inga*), non-native species with a long history in Central America (plantain, cacao, peach palm), and recent arrivals (orange, mango) (Zaldivar et al. 2002). The local diet includes 84 plant species—60 grown in “near” space (homegardens and fields that can be manipulated) and 24 grown in “far” space (natural forest from which products may be harvested sustainably but which cannot—according to traditional practices—be otherwise manipulated) (García-Serrano and Del Monte 2004). The genetic diversity of cassava (*Manihot esculenta*) found in these homegardens is higher than that found in commercial crops, and includes cultivars not found in South American indigenous homegardens (Zaldivar et al. 2004).

In summary, changes in neotropical vegetation over the past 10,000 years may be tied to at least five significant and possibly overlapping influences: fluctuations in climate (Farrera et al. 1999, Hughen et al. 2004, Islebe et al. 1996, Islebe and Sánchez 2002, Lozano-García et al. 2007), natural colonization of plants across the Central American Isthmus from both North and South America, fire (Avnery et al. 2011), loss of browsing pressure from mammalian megafauna (Johnson 2009), and direct human modification of the landscape by forest clearing, domestication of crop plants, and other agricultural practices (Iriarte 2011, Lane et al. 2008).

Colonial and Postcolonial Development

The fourth voyage of Columbus in 1502 included an oft-cited stop at the site of the current city of Limón, or rather at a small island (Isla Uvita) just offshore. The Europeans did not initially find this coastal area a particularly profitable region for exploitation, in addition to which they encountered strong resistance against their incursions from the indigenous people. The reader is guided to several treatments of the early history of Spanish settlement of the Caribbean area of Costa Rica as well as to discussions of more recent history (Molina and Palmer 2007, Palmer and Molina 2004, Ross and Capelli 2003). For the past 20 years, there has been much talk about the extent of the demographic collapse of indigenous populations due to diseases brought by the Europeans. Denevan (1992, 2003) and Newson (1993) estimated that as many as 90% of the indigenous people died upon contact with Europeans in ar-

reas as geographically widespread as the Caribbean Islands, Nicaragua, and the Amazon Basin. We consider the issue of human populations of the Caribbean lowlands below.

Recent History

Although many of the fine points of early human impact on the Caribbean lowland landscape have been lost (or hidden) in the mists of time, the record of land use change since the 1960s is remarkably complete. This knowledge is largely due to data from aerial photographs and remote sensing maps and also to concerted efforts to document the rapid changes that occurred during these years. This time period marks the beginning of at least three landscape-altering trends in Costa Rica that had a particularly strong impact on the Caribbean side of the country—rapid population growth, rampant deforestation, and incipient conservation efforts. One important point has already been made—that there are probably virtually no pristine or virgin forests in the Caribbean lowlands or anywhere in Costa Rica.

However, as recently as the early 1950s, most of the Caribbean lowlands were still covered in primary forest and older secondary forest, regrown from previous centuries of episodic and localized cutting, including felling trees for railroad ties in the nineteenth century.

Increased access to an area has invariably led to an increase in human settlement (Rosero-Bixby and Palloni 1998), from the construction of the Alajuela–Limón railroad at the end of the nineteenth century (Augelli 1987) to the completion of the San José–Guápiles highway through Parque Nacional Braulio Carrillo in the late 1970s (Sader and Joyce 1988) and to the completion of other roads over the past 30 years. Many areas in the Caribbean lowlands are still considered to be relatively inaccessible, and new roads continue to be planned and constructed even as the pressures from population growth and agricultural intensification increase. We treat the topics of deforestation, agriculture, and land conservation in separate sections below.

Current Conditions

The Physical Environment

Climate and Weather

The climate in the Caribbean lowland area is greatly influenced by the trade winds (*vientos alisios*) that blow onshore in a northeast to southwest direction. Local annual rainfall varies over a 2-fold range from about 2,500 mm to about 5,000 mm per year. Rainfall and other aspects of climate are also affected by the passage of the Intertropical Con-

vergence Zone (ITCZ) over the area twice a year. Rainfall is generally lower during the months of January through March, but the dry season is not as pronounced on the Caribbean side of the central mountain ranges as it is on the Pacific side (see also Herrera, chapter 2 of this volume).

The Costa Rican Instituto Meteorológico Nacional (IMN) has divided the Caribbean lowlands into six different zones, three of which border Nicaragua to the north (N1, N2, N3) and three of which run along the Caribbean coast (A1, A2, A3) (Fig. 16.3). The national data records indicate very similar temperatures in these zones (maximum, minimum, and median), but the rainfall patterns are

distinctly different (inset, Fig. 16.3). The zone with highest annual rainfall is in the north coastal zone N3 that includes the town of Guápiles (4,860 mm per year), with the driest zones at either end of the lowland stretch (2,722 mm around Upala and 2,470 mm in the zone that includes Cahuita and Sixaola). La Selva Biological Station is in a zone that receives an average of 3,710 mm per year, although the station itself receives 4,000 mm of rain per year (50-year mean annual rainfall).

Temperature and rainfall are the most commonly kept records for government and corporate weather stations, but there are many other relevant measures of weather and

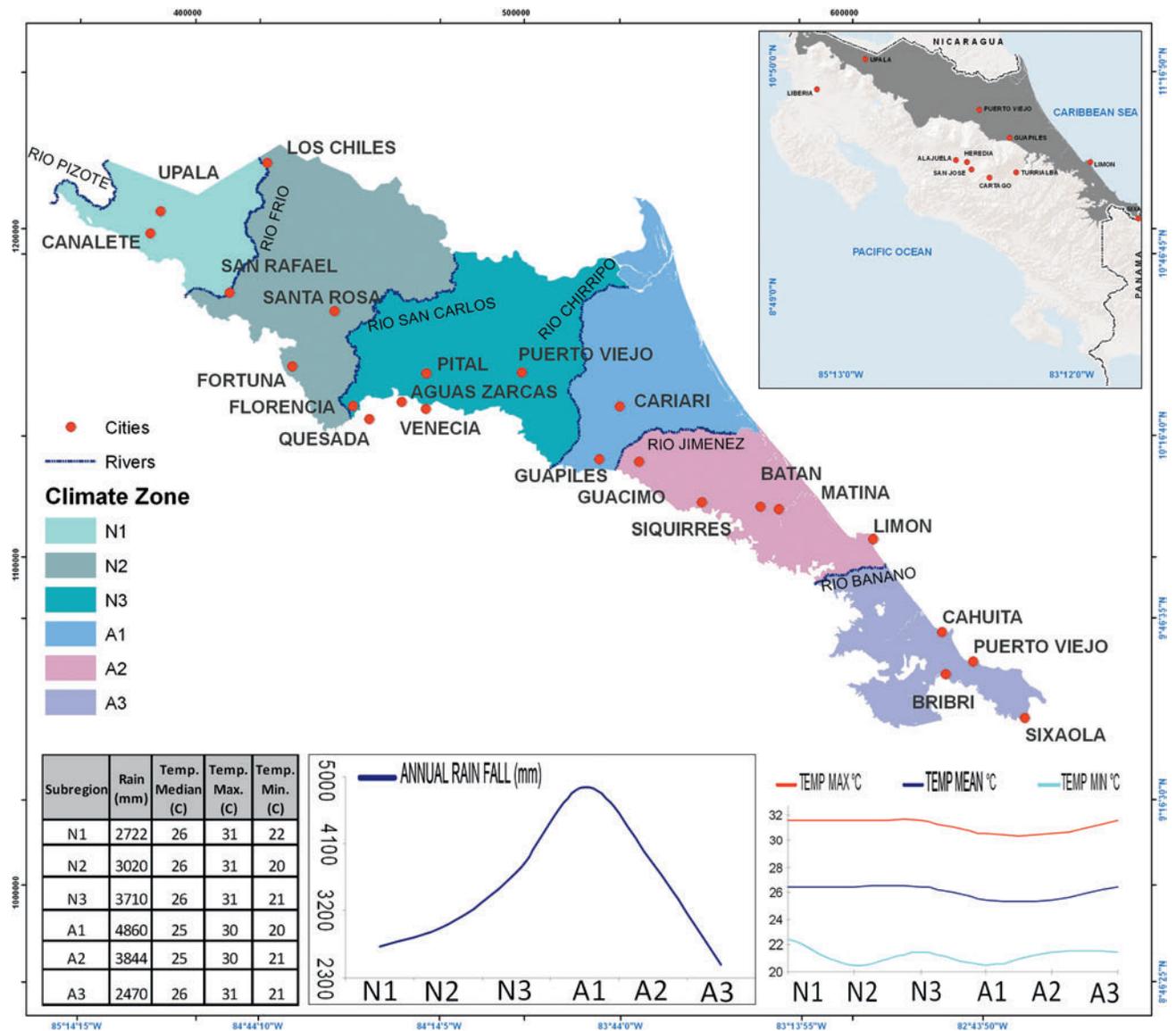


Fig. 16.3 Map of the climate zones of Costa Rica's Caribbean lowlands as defined by the National Meteorological Institute (IMN [Instituto Meteorológico Nacional]). The zones labeled N1, N2, and N3 are along Costa Rica's northern border with Nicaragua and the zones marked A1, A2, and A3 are the Atlantic sea margin areas. Temperature regimes are broadly similar across the entire area but annual rainfall has a distinct peak in the center of the region.

climate, including relative humidity, wind speed, wind direction, soil moisture, and PAR (photosynthetically active radiation). PAR is an important component of most climate models. Usually only the best-equipped weather stations maintain the full range of data. These additional records seem to be particularly prone to missing data, faulty or uncalibrated sensors, and human error in quality control (Clark and Clark 2011, Senna et al. 2005).

Patterns of tropical vegetation have been tied to climate at the medium and long-term temporal scales (from hundreds to millions of years) and also to a spatial scale of kilometers to hundreds of kilometers. On a geological time scale, the climate has fluctuated in ways that usually (but not always) pair relatively warm and moist conditions during one phase and cool and dry conditions during alternate phases (see Historical Overview, this chapter). In the tropical forests of today, the climate variables most frequently associated with specific vegetation types are temperature and rainfall. A mesoscale temperature gradient is generally associated with an altitudinal gradient (Cavelier 1996, Cavelier et al. 1999, Lieberman et al. 1996), whereas a rainfall gradient may be linked to or independent of elevation. Across lowland neotropical forests (eliminating the altitudinal variable), the floristic composition at a regional scale is nearly always linked to some aspect of water availability, although other factors such as soil fertility and historical accident may also play a role in creating and maintaining plant beta-diversity (Condit et al. 2002, Marques et al. 2011, Pyke et al. 2001, Toledo et al. 2011).

Primary productivity, biomass, global terrestrial carbon, and biodiversity are all concentrated in the tropics (Dirzo and Raven 2003, Dixon et al. 1994, Hartshorn 2006, Malhi et al. 2002, Melillo et al. 2002, Saugier et al. 2001). The impact of ongoing and future global climate change on tropical forests is therefore of great concern (Malhi et al. 2009). The likely effects of changes in temperature, increased atmospheric CO₂, and rainfall have attracted considerable attention (Beer et al. 2010, Clark 2004, Lewis et al. 2009, Körner 2009). Empirical data indicate that temperatures in the tropics have increased by about 0.26 degrees C per decade since the 1960s, largely driven by increases in nighttime minimum temperatures (Malhi and Wright 2004), and climate models predict continued trends in this direction (Cramer et al. 2004, Diffenbaugh and Scherer 2011, IPCC 2007, Malhi and Phillips 2004). If tropical forests are already near a high temperature threshold (Reed et al. 2012), a small increase in temperature could dramatically change forest-wide carbon stocks by mechanisms such as altering the balance between photosynthesis and respiration (Clark et al. 2003, Doughty and Goulden 2008), stimulating release of carbon from soils (Raich et al. 2006), or modifying

floristics in favor of liana abundance (Schnitzer and Bongers 2002, Wright et al. 2004). The likelihood of an atmospheric CO₂ fertilization effect in the tropics is still a matter of intense debate (Cernusak et al. 2011, Holtum and Winter 2010, Lewis et al. 2009).

Rainfall is an interesting case. Many climate models predict drought in the tropics (Cox et al. 2008, Neelin et al. 2006), but other models predict increased rainfall in areas that already receive high rainfall (the-rich-get-richer hypothesis) (Chou et al. 2009). Empirical data show declining rainfall across the tropics over the past 40 years, but this decrease is mostly concentrated in Africa and Asia (Malhi and Wright 2004). Still other models, and some recent empirical data, point to an increase in climate extremes that would intensify the severity of storms, floods, and droughts without necessarily changing annual rainfall (Aguilar et al. 2005, Jentsch et al. 2007, Marengo et al. 2011, Sun et al. 2007). Decrease in water availability on an annual or seasonal basis is of concern to tropical ecologists and climate scientists because many species of tropical trees and understory plants in lowland moist and wet forests of the neotropics are particularly drought-sensitive (Bunker and Carson 2005, Engelbrecht et al. 2007, Engelbrecht and Kursar 2003, Enquist and Enquist 2011, Feeley et al. 2011, Tyree et al. 2003).

In order to integrate information from a single well-documented site in the Caribbean lowlands of Costa Rica, we present the case of the La Selva Biological Station, situated at the base of Volcán Barva (Fig. 16.4). The weather records for the past 50 years from the meteorological stations on the property indicate an increase in temperature of 0.25 degrees C per decade, largely driven by increase in nighttime low temperatures (Clark and Clark 2011), consistent with global tropical patterns. The rainfall has been variable but has not changed over the 50-year period, maintaining a mean of 4,000 mm annually (Fig. 16.5). Interestingly, a shorter record (of the past 29 years) appears to show an increase in rainfall—but that increase disappears when the entire 50 year record is analyzed. A similar cycle is seen with the long-term weather records for Barro Colorado Island (BCI) in Panama (S. Paton, pers. comm.). Annual wood production in the La Selva old-growth forest is positively correlated with dry season rainfall and negatively associated with mean annual nighttime temperature for both stand-level (ten years of data) and focal tree species (24 years of data) analyses (Clark et al. 2010). In other words, the big trees grow less when the dry season is a bit drier than usual and also when the nights are a bit warmer than usual—and these two effects are independent. No evidence emerged for a carbon fertilization effect (Clark et al. 2010). Growth of La Selva trees is negatively correlated with global atmospheric CO₂ and with temperature (Clark



Fig. 16.4 View from the top of the CARBONO research tower on the SSO trail at the La Selva Biological Station, July 2010, in the middle of the rainy season. The view is looking southward towards San José (which is 55 km away in a straight-line distance on the other side of the peaks on the horizon). The base of the tower is at 97 m a.s.l. The peak on the left is Cacho Negro, a dormant volcano 2,100 m high. The peak on the far right is Volcán Barva, which provides the run-off for most of the streams and rivers of La Selva. Much of the forest in the middle ground is part of the San Juan–La Selva Biological Corridor.

Photo by Orlando Vargas.

et al. 2003), implying a causal linkage among tree growth, temperature, and atmospheric CO₂.

Some authors have predicted that high-elevation forests and low-elevation dry forest will be the most vulnerable of Costa Rica's ecosystems under conditions of climate change (Enquist 2002). Other authors predict “lowland biotic attrition” at La Selva and other lowland sites because, although lowland species can move upslope to track cooler temperatures, there is no source for species adapted to climates warmer than those of the existing lowlands (Colwell et al. 2008, Feeley and Silman 2010).

Soils

The parent material for most of the Caribbean lowland soils is derived from the episodic volcanic lava flows from the

mountains of the Central Cordillera, in addition to contributions made by volcanic mud flows (lahars) and volcanic ash (Sollins et al. 1994; Alvarado and Mata, chapter 4 of this volume). Even the sands of the Caribbean beaches are composed of volcanic material due to a process whereby: (1) the rivers have carried gravel, fine sediments, and ash from the volcanoes to the coast; and (2) coastal wave action has redistributed the material along the shore in a series of beach ridges (Nieuwenhuys and Kroonenberg 1994). Small sections of the coast are composed of ancient reefs, but these are the exception rather than the rule (Battistini and Bergoing 1984). Material from the offshore continental shelves apparently did not contribute significantly to the coastal sands. Coastal deposition has more than kept pace with coastal erosion in recent centuries, so that even with

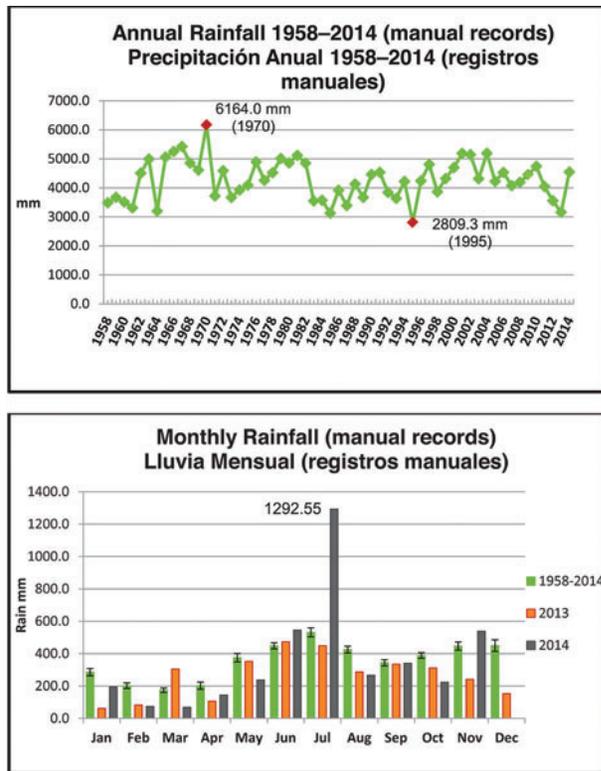


Fig. 16.5 Fifty-seven-year record of precipitation at the La Selva Biological Station. (Upper) Despite a wide range of wet years and dry years, the mean annual precipitation has held steady at 4,000 mm of rain for the entire duration of this record. (Lower) Monthly rains are expected to be high from May through December, with a dry season in January, February, and March. This pattern holds true as a mean over 50 years (green bars), but is subject to considerable variation from year to year. The year 2014 was characterized by a severe dry season and an extremely rainy wet season.

rising sea levels there has not been a net loss in beach area (Nieuwenhuysen et al. 1993).

The chemical composition of the parent material in the Caribbean lowland soils varies somewhat depending on which one of the several active volcanoes erupted and when it erupted. Reliable ages for the volcanic parent material have been difficult to establish, however. An estimate of 1.2 my for the oldest soils at La Selva (Alvarado 1990) is based on potassium argon dating, which is not a particularly accurate method for highly weathered material. The details of the rock-derived nutrients in these soils suggest a younger (less weathered) parent material and/or the existence of a tree-derived nutrient pump that brings silicon (an element usually depleted in weathered soils) from deep layers to the surface (Porder et al. 2006).

Various soil studies at La Selva and surrounding areas have contributed to our understanding of some of the big questions in tropical soil biology but they have also revealed an unanticipated level of complexity. Analyses of samples taken from the soil next to every grid post (distributed in

a 50 m by 100 m matrix across the La Selva landscape) formed the basis of the GIS soil map that is still in use today. In general the soils are weathered and deep, with moderately high organic matter content and a predominance of clay-sized particles of low bulk density (Parker 1994). Some of these soils were originally classified as Ultisols (Sollins et al. 1994) but have since been reclassified as Oxisols (Kleber et al. 2007). A treatment of soil taxonomy is beyond the scope of this chapter and the reader is guided to other publications (USDA–NRCS 1999; and see Alvarado and Mata, chapter 4 of this volume, for Atlantic soils in general).

La Selva’s soils are roughly grouped into the categories of residual (from the old lava flows at the “back” of the property at about 100 m elevation), old alluvial (old river terraces), and recent alluvial (current river terraces). Precipitation contributes sodium, chlorine, and magnesium from Caribbean marine aerosols (sea spray) as well as potassium and calcium from non-seasalt sources (Eklund and Pringle 1997). The chemicals and nutrients in the alluvium that is carried by streams and deposited on land during floods are derived from several sources, including low-solute local runoff and high-solute geothermal groundwater (Genereux and Pringle 1997), chunks of decomposing wood (Cadot and Wohl 2010, Cadot et al. 2009), and leaf-litter (Wood et al. 2005). Across La Selva, phosphorous content in old alluvial terrace soils is 3–4 times higher than similar values for residual soils, fine-root biomass decreases as soil fertility increases, and soil moisture decreases are stronger during dry periods in the residual than in the alluvial soils (Espeleta and Clark 2007). Down the slopes of the Barva and Poás volcanoes onto the lowland Caribbean terrain there is a strong elevational gradient in soil carbon isotopes, soil particle size, and other mineralogical variables in shallow samples—but this relation became less predictable at greater soil depths (Powers and Schlesinger 2002a,b). In experimental plantations, soil properties are also affected by the trees growing there (Russell et al. 2007). Studies of CO₂ flux in soil chambers dug to a 3 m depth on La Selva’s residual and old alluvial soils reveal differences between the two types of sites, with higher CO₂ levels emanating from the residual soils (Schwendenmann et al. 2003). CO₂ release was reduced when soil water content was either very high (saturated) or very low. Carbon stocks and microbial activity are substantial in subsoils down to 3 m depth (Veldkamp et al. 2003).

Until this point we have considered only terrestrial soils, but in tropical rainforests it is also critical to characterize the canopy soils. The canopy soils from four tree species on residual and alluvial soils at La Selva have higher N levels and higher fungi + bacteria richness than do paired samples of forest floor mineral soils; they are also more acidic in

both wet and dry seasons (Cardelús et al. 2009). These canopy soils have six times more carbon per unit mass than the forest floor mineral soils (Cardelús et al. 2009).

Despite the importance that forest floor soils, belowground processes, and canopy soil dynamics clearly must play in tropical terrestrial ecosystems, there are still large gaps in our understanding. For years ecologists have been concerned with the relation between soil properties and plant communities, the effect of land use changes on soil conditions, and the role of soil microorganisms in mediating basic processes. Recent attention has been directed towards the size of the belowground carbon pool and its sensitivity to climatic variation. One theme that emerges from the currently available information is the huge role that rainfall (annual and seasonal) and soil water content have on all of these processes, from the response of soils to land use changes (Powers et al. 2011) to the proliferation of fine roots belowground (Espeleta and Clark 2007) to the nutrients available to epiphytes in the upper reaches of the canopy (Cardelús et al. 2009).

Vegetation, Changes in Forest Cover, Forestry and Natural Regeneration, and Remote Sensing

In the following paragraphs we treat various aspects of vegetation in the Caribbean lowlands, including the plant communities of relatively intact systems, as well as the effects of alterations in the landscape caused by deforestation, forest fragmentation, agroforestry, and secondary forests. We conclude with a summary of the types of remote sensing techniques that have formed the basis of most of the landscape scale work covered herein.

Vegetation

The region that hosts the forests of the Caribbean lowlands of Costa Rica extends from the Peñas Blancas area of Guanacaste Province in the northwest to the mouth of the Río Sixaola in Limón Province in the southeast. Most of this region is quite flat from the Caribbean Sea to the foothills of the large mountain ranges, with scattered hills that do not rise above 500 m (Cerro Brujo 483 m, Cerro Copernon 400 m, Cerro Nispero 339 m, Cerro Olla de Carne 414 m). For this discussion we divide the area into three geomorphological units: lowlands, foothills, and valleys. Lowlands are the dominant unit (9,787 km²), foothills represent the second largest area (2,781 km²), and valleys cover the smallest area (1,279 km²).

Plant species lists for 16 different protected sites with forest cover (Fig. 16.6) were compiled from several different databases, including ATTA from INBio (the Costa Rican Instituto Nacional de Biodiversidad; [\[.ac.cr/\]\(http://atta.inbio.ac.cr/\)\), the Digital Flora of La Selva \(<http://sura.ots.ac.cr/local/florula4>\), and TROPICOS \(<http://www.tropicos.org/>\) from the Missouri Botanical Garden. Eight of the sites fit into our lowland category \(La Selva, Boca Tapada, Tortuguero, Cerros Chaparrón, Caño Negro, Upala, Barra del Colorado, and Guatuso\), four are foothills \(Hitoy Cerere, Fila Carbón, Rara Avis, and Bijagua\), and four are valleys \(Gandoca Manzanillo, Bananito, Cahuita, and Sixaola\). Every plant species was assigned a series of attributes, such as growth form, native vs. exotic origin, and commercial or medicinal use. The analyses provided below are based on these attributes.](http://atta.inbio</p>
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The known vegetation (based on the databases we used) of the entire region contains 196 families of vascular plants in 1,073 genera and 3,007 species. Of these species, we classify 1,269 species (42%) as herbs (including ferns), 760 (25%) as trees (including 26 hemiepiphytes, but excluding palms), 551 (18%) as bushes (including 66 epiphytes), 371 (12%) as vines, and 56 (2%) as palms.

At the family level, the most abundant families in the databases are Rubiaceae (189 spp.), Orchidaceae (163), Araceae (127), Melastomataceae (118), Piperaceae (101), Fabaceae/Papilionoidae (92), Poaceae (92), Asteraceae (71), Euphorbiaceae (65), and Malvaceae (65). The most speciose genera are *Piper* (73 spp.), *Psychotria* (50), *Miconia* (46), *Philodendron* (33), *Anthurium* (36), *Inga* (28), *Peperomia* (27), *Solanum* (26), *Calathea* (24), and *Pleurothallis* (24).

In considering these data and the graphs presented below regarding diversity of different plant life forms in different zones, it is important to keep in mind that the information is highly biased by the collecting effort at the various sites. Collecting effort is a function of number of hours spent as well as other factors such as the taxonomic interests and skills of the collector. A further complicating issue is the size of the area considered. A national park with well-defined boundaries may cover fewer hectares than another site that represents a more amorphous region, in which case the smaller area might be expected to have fewer species present. The La Selva Biological Station is probably the only site where the species accumulation curve is leveling off, and even at La Selva more than a dozen new species were added to the list in 2010.

Despite the cautions in comparing sites, there are several interesting findings and a few surprises. First of all, there are no species of the 3,007 total that are registered for all 16 of the sites from which our data are taken. This is not so surprising. However, there is no species that is known from more than nine of these sites. *Neea laetevirens* (Nyctaginaceae) and *Bactris hondurensis* (Arecaceae) are registered from nine sites and *Anthurium bakeri* (Araceae) and *Psychotria grandis* (Rubiaceae) are registered from eight sites.

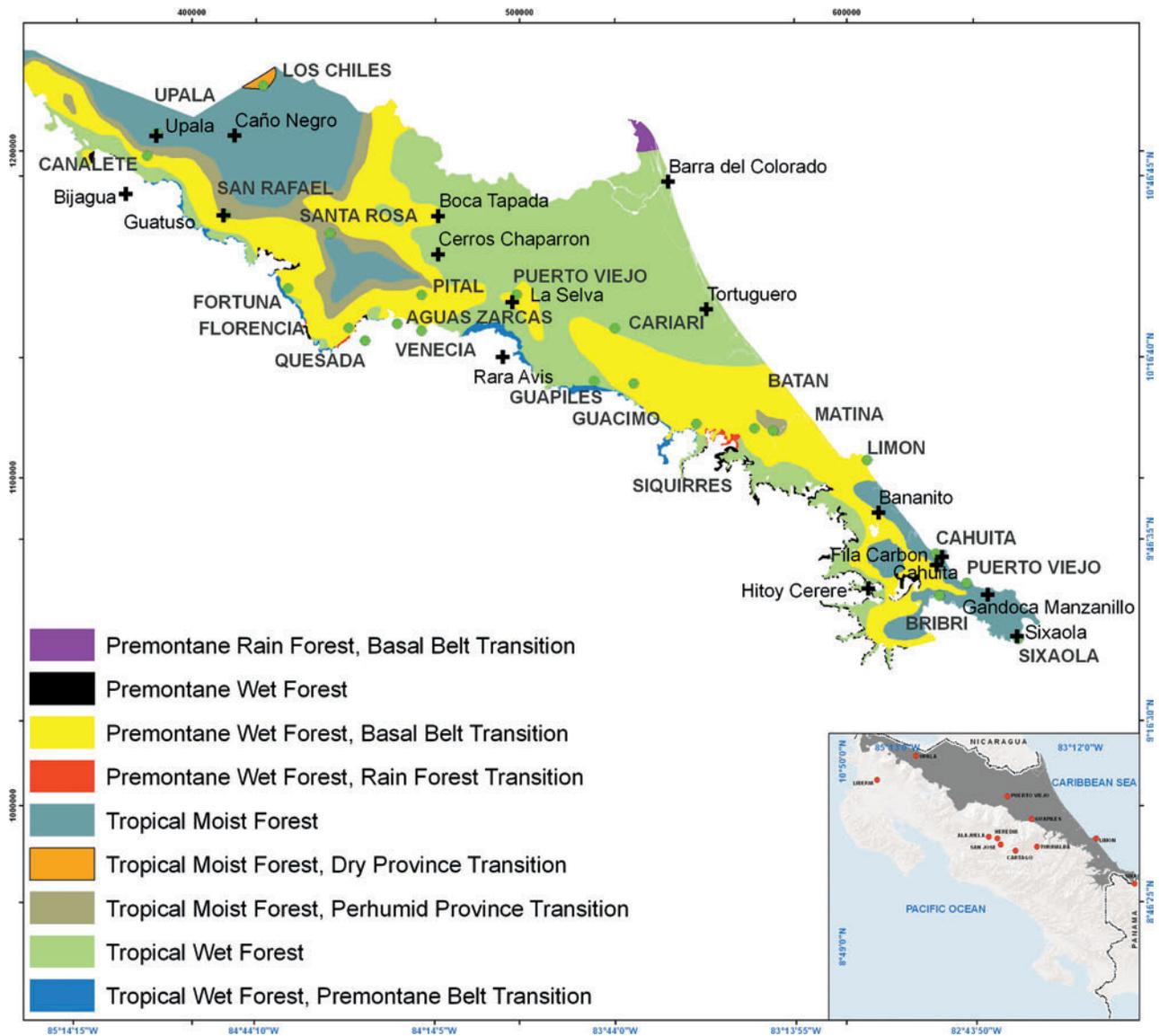


Fig. 16.6 Map of the locations of the plant collections used in the vegetation analysis. Additional color coding represents the Holdridge Life Zones covered herein.

Half of the species (1,508) are known from only a single one of the 16 sites. All other species are known from two to seven sites. This high degree of beta-diversity is striking but also in keeping with similar patterns seen across other Neotropical areas (Hartshorn and Hammel 1994, Marques et al. 2011, Pyke et al. 2001, Toledo et al. 2011).

The growth forms of the plant species considered by geomorphological unit follow the same general pattern that is seen in the complete database—herbs are the dominant type of plant, followed by trees, shrubs, vines, and palms.

If La Selva is taken as a nearly complete flora, it is instructive to consider patterns of vegetation specific to that site. Of the trees, the most abundant is *Pentaclethra maculosa*,

followed by the palms *Welfia regia* and *Socratea exorrhiza* and then by *Protium pittieri* and *Warszewiczia coccinea*. The dominant canopy emergent trees are *Dipteryx panamensis*, *Hymenolobium mesoamericanum*, *Lecythis ampla*, *Vochysia ferruginea*, *Hieronyma alchorneoides*, and *Ceiba pentandra*. The three dominant families in terms of species numbers are Orchidaceae, Araceae, and Bromeliaceae. Note that the dominant families at La Selva are not the same as those reported for the Caribbean lowlands as a whole. This may be a real phenomenon or it may be a function of the incomplete plant lists from the other sites.

At La Selva, the number of non-native vascular plants currently stands at 158. Many of these were introduced

intentionally (including crops planted by Leslie R. Holdridge in the 1950s and 1960s, and trees planted by Gary Hartshorn in the Arboretum in subsequent years). A few are recently escaped ornamental plants, including the highly invasive red banana (*Musa velutina*) that arrived at La Selva in 2003 or 2004.

La Selva has a nearly complete plant list, it represents a sizeable chunk (1,500 ha) of forest, and it is often used as a “control” or “intact” forest site in studies of nearby fragments. It is important to bear in mind, however, that La Selva cannot be considered pristine (see previous sections in this chapter). Indigenous people modified the landscape for at least 3,000 years and more recently the forest has felt the negative impact of the arrival of invasive species, modern climate change, pesticide residues, and a host of other influences.

Changes in Forest Cover

The production and harvesting of bananas, sugar cane, cattle, timber, non-timber forest products, heart of palm, cacao, and pineapple have all left their mark on the Caribbean lowlands in terms of deforestation and the resultant vegetation of modified landscapes (Fig. 16.7). Countrywide deforestation rates in Costa Rica reduced the coverage of primary forest from 67% (1940), to 56% (1950), to 45% (1961), to 32% (1977), to 17% (1983) (Sader and Joyce 1988). Several other estimates of Costa Rican deforestation rates are available based on slightly different methods (FAO 2000, Lutz 1993, Rosero-Bixby and Palloni 1998) but all

agree on the rapid conversion of primary forest to other uses during the 1960s, 1970s, and 1980s.

Deforestation occurred both on a small scale and on a large scale. Farmers took over a few hectares of land on an informal basis or were given land by the government and encouraged to “improve” their holdings (*mejoras*) by clearing them (Augelli 1987, Brockett and Gottfried 2002). These were years of a rapidly burgeoning human population—Costa Rica’s population quadrupled between 1950 and 2000 (Rosero-Bixby and Palloni 1998)—and the government actively promoted the settling at Costa Rica’s frontiers. At the same time that small holdings were expanding, large-scale deforestation was carried out for the purpose of cattle ranching and planting of agricultural crops. The amount of pastureland in Costa Rica doubled between 1950 and 1973 (Augelli 1987). Over time cattle ranching proved to be unsustainable or economically unfeasible in most areas of Costa Rica and many cattle pastures were abandoned or converted to other land uses by the 1990s.

These countrywide trends have been clearly evident in the Caribbean lowlands. Much of the banana plantation expansion occurred in the area northwest of Limón to the Río Sarapiquí basin, although banana plantations were also established to the south of Limón in the Estrella and Sixaola river valleys. In the northern area of the Caribbean lowlands 2,300 km² were deforested from 1961 to 1977 through clearing for a combination of agriculture, human colonization, roads, railroads, and logging (Pérez and Protti 1978). Detailed descriptions of changes in land use starting



Fig. 16.7 Aerial view in February 2011 (dry season) showing the border between pineapple fields and secondary forest on the property of the Costa Rican—Swiss Tropical Fruit Marketing Company in Horquetas, Sarapiquí. This property is known as Finca Roswita. Photograph taken on a joint photography mission of OTS, Panthera Costa Rica, and Lighthawk.

in the 1960s around La Selva in Puerto Viejo de Sarapiquí make illuminating albeit sobering reading (Butterfield 1994, Montagnini 1994, Read 1999). The population of the Sarapiquí canton (with La Selva near its center) skyrocketed from 2,169 people in 1950 to 45,218 people in 2000 (Schelhas and Sánchez-Azofeifa 2006).

To determine the loss of forest by ecological zone, Sader and Joyce (1988) digitized the black and white aerial photographs from various dates collected by the Costa Rican Ministry of Agriculture (MAG) (at a scale of 1:1,000,000) as well as the 1977 (Pérez and Protti 1978) and 1983 (Flores Rodas 1984) images created from aerial photography and Landsat MSS satellite data. They overlaid these maps with a digitized 1:750,000 scale map of ecological zones (Tosi 1969) to show that most of the remaining Caribbean lowland forest in 1983 pertained to the Tropical Wet, Tropical Moist, and Premontane Wet life zones, in that order. The highest rates of forest disturbance (8.8% to 16.4%) occurred in these life zones during the period from 1977 to 1983. Between 1940 and 1983, Costa Rica lost 78% of its Tropical Wet forest, most of which was in the Caribbean lowlands. Especially high rates of clearing were recorded on the 0–5% slope category in the northeastern Caribbean lowlands. Another land-use evaluation based on agricultural censuses and satellite images concluded that in the year 2000 forest in the Caribbean lowlands was restricted to lands with poor biophysical characteristics (mostly in national parks) and that “banana plantations have claimed the best soils in flat, non-flooded areas” (Veldkamp et al. 2001).

More recent publications have revealed additional information on a localized geographic scale. Sánchez-Azofeifa et al. (2003) used data acquired by the Landsat TM sensor during 1996 and 1997 to analyze forest changes in buffer strips of one and 10 kilometers in width around all protected areas. These data indicated that deforestation was “under control” in the one kilometer buffer in protected areas within most of the Caribbean lowlands, but that widespread deforestation within the 10 km buffer around the Tortuguero National Park in the Caribbean coastal area north of the city of Limón was turning the park into an isolated island of forest within an agricultural landscape. In the area near EARTH University in Guápiles, as in many other regions of the Caribbean lowlands, abandoned pasture lands (many of which had become young secondary forests) are undergoing a wave of conversion to pineapple plantations (Joyce 2006).

An additional, and surely unintended, source of deforestation in the Caribbean lowlands during the 1980s and early 1990s is associated with projects on forest inventory and sustainable forestry. The original hope was that primary and older secondary forests could be logged selec-

tively to provide marketable timber and enough income for the landholders in order to prevent the conversion of the forests to agricultural and grazing lands (Finegan 1992, Howard 1995, Howard and Valerio 1996). In many cases, however, the plans for selective logging did not work out as intended and the forest designated for several of these forestry projects has now almost all been cleared (Rodríguez unpublished data) because the logging practices proved not to be sustainable, because the access roads built in the zone greatly increased the vulnerability of these trees (these were the years before the passage of the Forestry Law), or because of other factors. Analyses of two different forestry projects are presented in the Forestry section below.

Costa Rica’s deforestation rates have declined in recent years, due partly to protection derived from the Forestry Law of 1996 (De Camino et al. 2000), which both prohibits the transformation of land that was forest in 1996 to any other sort of land cover *and* provides Payment for Environmental Services (using the acronyms PES in English and PSA [*pago por servicios ambientales*] in Spanish) for intact forest. On lands adjacent to Parque Nacional Braulio Carrillo and La Selva, the rates of deforestation went from 19.4% per year (8,319 hectares lost) between 1986 and 1996 to 6.7% per year (2,332 hectares lost) between 1996 and 2000 (Schelhas and Sánchez-Azofeifa 2006). Any young forest regrown since 1996 is not protected by the Forestry Law, and it is these areas that are under pressure from expanding pineapple agriculture in the lowlands.

Forestry and Natural Regeneration

Two main forestry activities have occurred during the past decades in areas outside the protected area network in the Caribbean lowlands—selective logging and forestry plantations—and both have economic and conservation importance.

Natural Forest Management

Natural forest management (selective logging) in Costa Rica started as a regulated activity in 1969 (Law 4465). It was not until 1996 however, with Forestry Law 7575, that this activity became highly regulated by the Forestry Authority of the State (De Camino et al. 2000) with a more standardized methodology following principles, criteria, and indicators of forest sustainability. In order to assess the potential value of natural forest management plans (NFMPs) in biodiversity studies, Arroyo-Mora collected 130 NFMPs submitted to the Ministerio de Ambiente y Energía (MINAE) between 1995 and 2005. The parcels were scattered over an area of 65,234 ha of Caribbean lowlands of the Cordillera Volcánica Central Conservation Area (CVCCA). Sixty-two of the 130 NFMPs were approved by MINAE and the to-

tal area under management with these forest parcels was 1,840 ha, with most of the forest management carried out in the largest patches within the study area. More NFMPs were submitted and approved in the first half of the 1995–2005 period in comparison to the second half, with 1997 and 1998 as the peak years for NFMPs submitted and approved (Arroyo-Mora et al. 2009). A potential explanation for the lower number of plans submitted in the second half of the period is that incentives shifted from natural forest management towards PSA after the passage of the Forestry Law in 1996. As is the case with plantations (see below), the future of natural forest management is uncertain.

An additional example highlights the fate of the internationally funded forestry projects from this era. Aerial photographs acquired in January 1983 were interpreted to stratify a 14,489 ha forest area between the Río Sucio on the north and the Braulio Carrillo National Park on the south, the Río Puerto Viejo on the east, and the Río Guacima on the west into six categories on the basis of the amount of forest disturbance and canopy height. This forest inventory project was funded by the USAID (Programa CORENA GCR-AID-515-T-032) and conducted in conjunction with the Ministry of Agriculture and, at the time, was known as the 032 Project. Tree measurements were made on 74 one-hectare plots that were randomly located in the six forest disturbance strata. Inventory results were summarized by species and showed that *Pentaclethra maculosa* (the dominant tree at La Selva) represented the greatest biomass of any tree across all of these 74 plots. A follow-up study was mounted three years later, funded by NASA and conducted with the ITCR School of Forestry, to verify the status of these parcels and to use the 032 Project tree measurement data to estimate the aboveground biomass in the plots that were not altered (Sader et al. 1989). By the end of 1986, however, 29 of the plots had been altered through logging and/or clearing.

Plantations

Forestry plantations, as a productive activity, started in Costa Rica at the end of the 1960s, and by 1979 there were 171,000 hectares of forestry plantations in the country (Arias 2004). From the Costa Rican Forest Cover Assessment for the year 2005, Calvo et al. (2006) report a total of 100,547 hectares of plantations for the country, based on data from NGOs, the Forestry Authority of the State, and private companies. From this total, 20,435 ha are located in the Caribbean lowlands, corresponding to approximately 20% of the area of the country's timber plantations. The primary stock of tree species that provide the current and future timber products from plantations encompasses 19 species, of which the most important (in terms of area that the plantations cover) are *Tectona grandis*, *Gmelina*

arborea, *Cordia alliodora*, *Vochysia guatemalensis*, and *Hieronyma alchorneoides*. *T. grandis* and *G. arborea* plantations cover 78.3% of the total area (Corella 1999). Seventy-three percent of these plantations were established between the years 2000 and 2006, whereas the other 17% were created between the years 1992 and 2000. Currently, at the national level and probably also at the local level in the Caribbean lowlands, older plantations have been harvested and replaced by cash crops such as pineapple, sugar cane, and bananas (Calvo 2008), resulting in an uncertain future for forestry plantations in general.

In the Caribbean lowlands, reforestation with exotic species (gmelina and teak) and research with native species (Butterfield and Espinoza 1995, Butterfield and González 1996, Montagnini et al. 1995) developed almost simultaneously. Plantations with gmelina and teak were favored for their fast growing characteristics, as well as the low maintenance of gmelina and the good market prices of teak. Studies with native tree species, which began in the mid-1980s in and around the La Selva Biological Station with the TRIALS project, showed the adaptability and growth potential of several native species in degraded soils and abandoned areas, providing a base for the development of reforestation programs with small and medium farmers in the region. Recent studies on native plantations have focused on their potential for carbon sequestration (Redondo-Brenes and Montagnini 2006, Russell et al. 2010).

Secondary Forests

During the years that deforestation rates slowed, secondary forest regeneration from abandoned cattle pastures and agricultural plots increased. Between 2000 and 2005, secondary forest regrowth in Central America, as defined by the United Nations Food and Agriculture Organization (FAO; 2007), was estimated to be 2.4% (Asner et al. 2009). In Costa Rica, over 2,000 km² of forest regrowth occurred between 1960 and 2000 (Arroyo-Mora et al. 2005), mostly in hilly regions, resulting in net afforestation at the country scale. At the turn of the century in Costa Rica, secondary forests covered an estimated 400,000 ha (Berti 2000), although this number may be low because of imprecise techniques to detect secondary forest in tropical dry and moist forests both on the ground and from remote sensing data (Calvo et al. 2006).

In Costa Rica's Caribbean lowlands, the regrowth of secondary forest after deforestation, some of it haphazard and some of it managed, has resulted in a mosaic of forest patches of different sizes, ages, distance from nearest seed source, and history of use before regrowth. At the turn of the century, in the Huetar Norte region (in the area between the La Selva Biological Station and the Río San Juan),

the size of secondary forest fragments ranged from four to 60 hectares, with a mean of 12.6 hectares (Berti 2000). These parcels of secondary forest created an ideal system of plots for analyzing tropical forest regeneration, community assembly, and species richness in this zone. In general, these studies found that the Caribbean lowland soils are more fertile than lowland volcanic soils in other parts of the world, that forest regeneration occurs more rapidly than had previously been anticipated, and that the rules of plant community reassembly are more complex than had been expected.

In the early 1990s secondary forest regeneration was expected to accumulate to levels of old-growth forest species richness, basal area, canopy height, and stem density within 30 years (Brown and Lugo 1990, Finegan 1996), but with distinct species composition as a result of the filtering effect of initial site conditions on propagule dispersal, seedling establishment, and subsequent growth and survival of local seeds (Finegan 1996). At this time, however, detailed information about the species composition of various ages of secondary forests in the region remained scarce. Existing studies had focused on large trees >10 cm DBH (diameter at breast height) in order to evaluate potential timber resources (Werner 1985, Finegan and Sabogal 1988, Guillén 1993). Guariguata et al. (1997) compiled the first extensive investigation of differences in woody vegetation structure and composition of seedlings, saplings, and trees between and within old growth and post-agricultural secondary forest stands of 16–18-year-old growth at and around La Selva Biological Station. They demonstrated that stem density and basal area for seedlings, saplings, treelets, and trees were similar between old growth forest and secondary sites. Plant species richness was consistently lower in intermediate-aged secondary stands because of greater dominance by fewer species (Guariguata et al. 1997, Boucher et al. 2001). In later resurveys of the same forest stands, plant species richness was found to attain levels similar to old growth forests within 30 years (Chazdon et al. 1998, Capers et al. 2005, Letcher and Chazdon 2009a). In contrast, species richness of lianas showed no change or a slight decline with forest age, depending on the method of assessment (Letcher and Chazdon 2009b).

Aboveground biomass also follows a similar trend, achieving comparable levels with old growth forest after 21–30 years of abandonment, emphasizing the high conservation value of secondary forests (Letcher and Chazdon 2009a, Norden et al. 2009). In fact, as much as 70% of species found in secondary forest stands in the area were shown to have commercial and medicinal uses (Chazdon and Coe 1999), aside from their value in the provision of ecosystem services. Across secondary forest stands there is a clear and

expected trend of successional change in forest structure and composition, but local site factors result in variations in species composition and rates of changes among stands (Chazdon et al. 2007). Small-scale local variation in soil fertility and compaction has affected tree species distributions in both old growth and secondary forest stands (Clark et al. 1999, Guariguata and Dupuy 1997, Herrera and Finegan 1997), which, owing to species-specific effects, has influenced understory floristic composition and species richness (Finegan and Delgado 2000).

Other studies of secondary forests in this region focus on characterizing the structure and composition of these forests (Guariguata et al. 1997, Redondo-Brenes et al. 2001), describing the dynamics of the forest at different ages since abandonment (Vílchez et al. 2004), or determining the economic value of secondary forest as carbon sinks (Ramírez et al. 2002). The small spatial extent of these studies limits our ability to extrapolate their results to the entire region.

The presence of several large old growth forests in the region, the remnant trees in secondary forest stands at the time of abandonment (Guariguata et al. 1997), and the abundance of seeds in the soil seed bank—substantially higher than in nearby old growth forest (Dupuy and Chazdon 1998)—as well as the presence of seed dispersers (Slocum and Horvitz 2000, Chazdon et al. 2003), have all contributed to a rapid recovery of tree basal area, woody seedling abundance, and species richness (Chazdon et al. 1998, Nicotra et al. 1999, Chazdon et al. 2005, Capers et al. 2005, Letcher and Chazdon 2009a). Secondary forest reassembly is converging with old growth community composition (Norden et al. 2009), though investigations of community phylogenetic structure during succession have found strong phylogenetic overdispersion at multiple scales (Letcher 2010).

After 20–25 years of development, when these stands reach the point of stem exclusion, aboveground carbon stocks have been calculated to be equivalent to those in primary forests of the region (Clark and Clark 2000). Early findings indicated that species-specific differences in root architecture result in differential nitrogen and phosphorus exploitation. Nutrient use efficiency, productivity, and nutrient residence times also showed species-specific responses (Hiremat et al. 2002). Shifts in nitrogen uptake in bromeliads (using isotope ratio) indicate that 77–80% of the nitrogen in small individuals originates from the atmospheric sources, whereas in larger individuals as much as 64–72% was soil-derived (Reich et al. 2003), adding a further layer of complexity to rainforest research. Various combinations of species identity and cutting rotations in monoculture and polyculture plots with native tree and monocot species produced highly variable results in total soil organic

carbon (TSOC) levels after 10 years. TSOC calculations ranged from loss of 24% (0.9 mg/ha/year) to an increase of 14% (0.6 mg/ha/year) with root C:N ratio and fine-root growth accounting for most of the changes in soil carbon sequestration (Russell et al. 2004).

In later investigations using the same plots, Russell et al. (2010) found that after 16 years, species-specific variations were significant for partitioning of net primary production (NPP) among biomass components, tissue turnover rates, aboveground and belowground biomass, and detritus and also in belowground C cycling processes such as soil respiration, heterotrophic respiration, and belowground NPP. Such species-specific trends were also recorded for independent plantation stands at La Selva for litterfall and macronutrient content (Montagnini et al. 1993). Arbuscular mycorrhizae, spore abundance, and host tree species showed species-specific signals (Lovell and Ewel 2005). Total NPP and soil organic carbon at 1 m depth showed no species effects (Russell et al. 2010). Collectively these findings highlight that at small scales, species-specific signals and plantation diversity richness impact biogeochemical cycling and that predictive models need to incorporate these biotic variations. In terms of carbon sequestration, intermediate-aged plantation plots at La Selva indicate rates of carbon sequestration of $5.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ over 17 years (Russell et al. 2010). These findings are comparable with results at the same location in younger stands on different soils (Redondo-Brenes and Montagnini 2006) and in older stands of exotic species in Panama (Kraenzel et al. 2003).

Remote Sensing

Many of the earliest studies and projects described in the preceding sections were based on landscape-level studies with data from aerial photography and Landsat satellite images. The main problem with the use of data acquired by sensors (cameras and scanners) that measure reflectance from the surface for the Caribbean lowlands is the persistent cloud cover over the Caribbean Lowland region. For this reason many of the images acquired by these surface reflectance measuring satellite sensors for the Caribbean lowlands are not free of clouds, especially in the northwestern portion of the zone.

One solution to the cloud problem is the use of Synthetic Aperture Radar (SAR) sensors that measure backscatter at microwave frequencies and are not affected by cloud cover. However, until the recent launch of the Japanese PULSAR, data acquired with other SAR sensors in spacecraft (JERS-1, Radarsat, SRTM) had very coarse spatial resolution. SAR data acquired in Costa Rica by aircraft (Wu and Joyce 1988, Elizondo and Zamora 1998, Joyce 2006) have been acquired only over scattered selected areas.

Although coverage did not include the northwestern region of the Caribbean Lowlands, where clouds are the most persistent, most coverage included the area around the La Selva property. Since energy transmitted from improved SAR sensors can penetrate the forest vegetation, the measurement of SAR backscatter has the potential to be used to assess forest structure and make estimations of the aboveground biomass. L-Band SAR data were acquired for a portion of the Caribbean Lowlands (January and February 2010) and are posted for downloading.

In addition to improvement in the technology of SAR sensors since 2000, there has been significant improvement in the technology for hyperspectral and laser (Lidar) sensors. Both of these technological advances have been used to great effect in analyses of the forests at the La Selva Biological Station and the surrounding areas, including the Sarapiquí watershed and the Caribbean portion of the Mesoamerican Biological Corridor (Arroyo-Mora et al. 2008, Clark et al. 2005, Drake et al. 2002a,b, 2003, Dubayah et al. 2010, Zhang et al. 2006).

In summary, remotely sensed data have been analyzed to produce maps of the forest vegetation and for studies of land use change (Joyce 2006) throughout the Caribbean lowlands. Various other studies with remotely sensed data have provided information on forest parameters and forest function in selected areas in the Caribbean lowlands, especially for the forest on the OTS-administered La Selva Biological Station property and vicinity. New sensor technology and improved analytical techniques, especially for hyperspectral, SAR, and Laser (Lidar) sensors, also hold great potential for providing additional information for assessment of forest structure, biomass, and species composition.

Animals—Invertebrates and Vertebrates

Costa Rica has a long and robust tradition of taxon-based animal research. In the Caribbean lowlands, much of the invertebrate work has been of a taxonomic and biogeographic nature, with special attention being paid to ants, butterflies and moths, and beetles. Among the vertebrates, birds, frogs, and bats have been particularly well-studied. In recent years there has been a proliferation of studies of plant–animal interactions in the general areas of herbivory, seed dispersal, pollination, and trophic relations. DNA barcoding has come into its own as a technique used in invertebrate (as well as plant) studies. Genomic and other molecular and biochemical techniques are now routinely paired with field observations to provide an integrated perspective on the lives of these tropical animals. Most of the reviews in the following sections are based on the published literature. The discussion of the Caribbean lowland fishes is derived

largely from the research and personal observations of one of the coauthors (R.C.C.).

Invertebrates

The most comprehensive invertebrate inventory project in the Caribbean lowlands was the 14-year ALAS (Arthropods of La Selva) enterprise led by Rob Colwell and Jack Longino. During this time period (starting in 1991), hundreds of thousands of specimens were collected, processed, and deposited in museums around the world, including at Costa Rica's INBio (National Biodiversity Institute) (<http://purl.oclc.org/alas>). The ALAS project also developed the software programs EstimateS and Biota, used for calculating biodiversity and for managing biodiversity databases, respectively (Colwell 2005, Colwell et al. 2004, Gotelli and Colwell 2001). A long-term tropical butterfly project run by Phil DeVries and Isidro Chacón moved its Costa Rican center of operations from La Selva to the nearby Tirimbina Biological Reserve and continues to provide country-wide information on lepidopteran diversity (Chacón and Montero 2007, DeVries 1979, 1997, DeVries et al. 2012, Walla et al. 2004). Angel Solís from INBio and his colleagues have been monitoring dung beetle populations throughout the country for several decades, with a 35-year record for La Selva (Escobar et al. 2008). Nematode diversity in different soil types at La Selva (including canopy soils) has recently become a noteworthy topic (Powers et al. 2009). Treatments of the more ecological invertebrate projects are to be found in the Plant-Animal Interactions sections below.

Fish

Although the species comprising the fish fauna of the Caribbean lowlands of Costa Rica have been identified, most aspects of their biology in the wild are poorly studied (e.g., see Pringle et al., chapter 18 of this volume). The total biodiversity of fishes in the Caribbean lowlands is minute (Bussing 1998; Bussing 1994, Appendix 4 lists 43 species at the La Selva Biological Station) compared to the thousands of species in the Amazon (1300++; Goulding 1980), and the fish fauna is dominated by just a few families—the cichlids (Cichlidae), the characins (Characidae), and the livebearers (Poeciliidae). Even these families are represented by only a handful of species each. The various catfish families that achieve incredible diversity further south (e.g., the pimelodid catfishes, the callichthyids, and the suckermouth catfishes of the family Loricariidae) are represented by just three species of pimelodids. Other families have token representation, including single species of the Carcharhinidae, Elopidae, Gobiesocidae, Rivulidae, Atherinidae, Synbranchidae, Synbranchidae, Haemulidae, Centropomidae,

Eleotridae, and a couple of members of the Mugilidae and Gobiidae (Table 16.1).

Despite low biodiversity, the ichthyofauna has many fascinating characteristics. For example, the pipefish *Pseudopallus mindii* is found near the coast but has also been recorded at least twice at La Selva (Bussing 1998; Coleman, personal observation), a full 75 km from the coast, and certainly a long swim for a small pipefish. The freshwater clingfish (*Gobiesox nudus*) is from a family, Gobiesocidae, often associated with the intertidal zone of the eastern Pacific Ocean including Washington, British Columbia, and Alaska. Fishes such as the American eel (*Anguilla rostrata*) and the pike killifish (*Belonesox belizanus*) are considered distinctly coastal and have wide latitudinal ranges on the Atlantic coast north and south of Costa Rica. The blackbelt cichlid, *Theraps maculicauda*, always appears to be within sight of the surf line. Other “coastal” fish, such as the tarpon (*Megalops atlanticus*), penetrate far upstream into the lowlands. The bigmouth sleeper (*Gobiomorus dormitor*) is usually seen near the coast but can be found far inland at La Selva. It is not known whether individual sleepers move this distance—given their sedentary lifestyle, it seems unlikely.

The distribution of species in the region is no doubt a product of the overall river patterns in the region. There appear to be three major assemblages. The large river bounding the north side of the region is the Río San Juan, which flows from Lake Nicaragua into the Caribbean. Because this large river drains Lake Nicaragua, it brings fishes that are not typically found in the rest of the zone into the northern edge of the region. For instance, several cichlids such as the midas cichlid *Amphilophus citrinellum* and the jaguar cichlid *Parachromis managuense* are common in the Lake and are also found at the river mouth at the far northeastern corner of the lowlands at Refugio Nacional de Vida Silvestre Barra del Colorado. In fact, it is interesting that these species have not penetrated further south. The bull shark *Carcharhinus leucas* and the sawfish *Pristis pristis* are in the Lake and in the Río San Juan, and extremely rarely a bull shark will swim up the Río Sarapiquí to be spotted at La Selva. Gars (*Atractosteus tropicus*) are found in the Río San Juan and are common in the sluggish waters of Caño Negro. We cannot compare the fishes of the Costa Rican lowlands to the fishes north of the Río San Juan because that portion of Nicaragua is largely unstudied with regard to fishes.

The bulk of the northern portion of the lowlands is drained by several large river systems that originate in the volcanic highlands to the west and flow roughly north or northeast to the Río San Juan. These include, from west

Table 16.1. List of Fishes of the Caribbean Lowlands of Costa Rica Ordered per Sector

Family	Species	English Name	Spanish Name
Fishes of the Río San Juan sector			
Carcharinidae	<i>Carcharhinus leucas</i>	bull shark	tiburón
Pristidae	<i>Pristis pristis</i>	sawfish	pez sierra
Lepisosteidae	<i>Atractosteus tropicus</i>	gar	gaspar
Clupeidae	<i>Dorosoma chavesi</i>	shad	sabaleta
Characidae	<i>Astyanax nasutus</i>	Colcibolca tetra	sardina lagunera
Gymnotidae	<i>Gymnotus maculosus</i>	knifefish	madre de barbudo
Pimelodidae	<i>Rhamdia nicaraguensis</i>	catfish	barbudo
Rivulidae	<i>Rivulus isthmensis</i>	Isthmian rivulus	olomina
Poeciliidae	<i>Alfaro cultratus</i>	alfaro	olomina
	<i>Brachyraphis parismina</i>	olomina	olomina
	<i>Neoheterandria umbratilis</i>	olomina	olomina
	<i>Phallichthys amates</i>	merry widow	olomina
	<i>Phallichthys tico</i>	olomina	olomina
	<i>Poecilia gillii</i>	molly	olomina
	<i>Poecilia mexicana</i>	shortfin molly	olomina
Atherinidae	<i>Atherinella hubbsi</i>	silverside	sardina
Synbranchidae	<i>Synbranchus marmoratus</i>	marbled swamp eel	anguila de pantano
Cichlidae	<i>Amphilophus citrinellus</i>	midas cichlid	mojarra
	<i>Archocentrus centrarchus</i>	flier cichlid	mojarra
	<i>Archocentrus nigrofasciatus</i>	convict cichlid	congo
	<i>?Astatheros alfari</i>	pastel cichlid	mojarra
	<i>Astatheros longimanus</i>	redbreast cichlid	cholesca
	<i>Herotilapia multispinosa</i>	rainbow cichlid	mojarrita
	<i>Parachromis dovii</i>	wolf cichlid	guapote
	<i>Parachromis managuensis</i>	jaguar cichlid	guapote tigre
Gerreidae	<i>Eugerres plumieri</i>	mojarra	mojarra prieta
Haemulidae	<i>Pomadasys croco</i>	Atlantic grunt	roncador
Mugilidae	<i>Agonostomus monticola</i>	mountain mullet	tepemechin
Gobiidae	<i>Awaous banana</i>	lamearena	lamearena
Fishes of the coastal sector			
Elopidae	<i>Megalops atlanticus</i>	tarpon	sábalo real
Anguillidae	<i>Anguilla rostrata</i>	American eel	anguila
Poeciliidae	<i>Belonesox belizanus</i>	pike killifish	pepesca gaspar
	<i>Poecilia mexicana</i>	shortfin molly	olomina
Atherinidae	<i>Atherinella hubbsi</i>	silverside	sardina
Cichlidae	<i>?Amphilophus citrinellus</i>	midas cichlid	mojarra
	<i>?Archocentrus centrarchus</i>	flier cichlid	mojarra
	<i>Theraps maculicauda</i>	blackbelt cichlid	pis pis
Centropomidae	<i>Centropomus parallelus</i>	fat snook	calva
	<i>Centropomus pectinatus</i>	blackfin snook	gualaje Atlántico
	<i>Centropomus unidecimalis</i>	common snook	róbalo
Carangidae	<i>Caranx latus</i>	jack	jurel
Gerreidae	<i>Eugerres plumieri</i>	mojarra	mojarra prieta
Haemulidae	<i>Pomadasys croco</i>	Atlantic grunt	roncador
Eleotridae	<i>Dormitator maculatus</i>	fat sleeper	guarasapa
	<i>Eleotris amblyopsis</i>	sleeper	pez perro
	<i>Eleotris pisonis</i>	spiny-cheek sleeper	pez perro
	<i>Gobiomorus dormitor</i>	big-mouth sleeper	guavina
Paralichthyidae	<i>Citharichthys spilopterus</i>	flounder	lenguado
	<i>Citharichthys uhleri</i>	flounder	lenguado
Achiridae	<i>Trinectes paulistanus</i>	sole	lenguado redondo
Fishes of the central sector			
Characidae	<i>Astyanax aenus</i> (= <i>fasciatus</i>)	banded tetra	sardina
	<i>Bramocharax bransfordii</i>	longjaw tetra	sardina picuda
	<i>Brycon guatemalensis</i>	machaca	machaca
	<i>Bryconamericus scleroparius</i>	creek tetra	sardina de quebrada
	<i>Carlana eigenmanni</i>	carlana tetra	sardinita
	<i>Hypessobrycon tortuguerae</i>	Tortuguero tetra	sardinita
	<i>Roebooides bouchellei</i>	glass headstander	sardinita
Gymnotidae	<i>Gymnotus cylindricus</i>	knifefish	madre de barbudo
Pimelodidae	<i>Rhamdia nicaraguensis</i>	catfish	barbudo

continued

Table 16.1. Continued

Family	Species	English Name	Spanish Name
	<i>Rhamdia guatemalensis</i>	catfish	bardudo
	<i>Rhamdia rogersi</i>	catfish	barbudo
Rivulidae	<i>Rivulus isthmensis</i>	Isthmian rivulus	olomina
Poeciliidae	<i>Alfaro cultratus</i>	alfaro	olomina
	<i>Brachyrhaphis holdridgei</i>	olomina	olomina
	<i>Brachyrhaphis olomina</i>	olomina	olomina
	<i>Brachyrhaphis parismina</i>	olomina	olomina
	<i>Neoheterandria umbratilis</i>	olomina	olomina
	<i>Gambusia nicaraguensis</i>	mosquito fish	olomina
	<i>Phallichthys amates</i>	merry widow	olomina
	<i>Phallichthys quadripunctatus</i>	olomina	olomina
	<i>Phallichthys tico</i>	olomina	olomina
	<i>Poecilia gillii</i>	molly	olomina
	<i>Priapichthys annectens</i>	olomina	olomina
Atherinidae	<i>Atherinella chagresi</i>	silverside	sardina
	<i>Atherinella hubbsi</i>	silverside	sardina
Gobiesocidae	<i>Gobiesox nudus</i>	clingfish	chupapiedra
Syngnathidae	<i>Pseudophallus mindii</i>	pipefish	pez pipa
Synbranchidae	<i>Synbranchus marmoratus</i>	marbled swamp eel	anguila de pantano
Cichlidae	<i>Archocentrus nigrofasciatus</i>	convict cichlid	congo
	<i>Archocentrus septemfasciatus</i>		mojarra
	<i>Astatheros alfari</i>	pastel cichlid	mojarra
	<i>Astatheros rostratus</i>		
	<i>Herotilapia multispinosa</i>	rainbow cichlid	mojarrita
	<i>Hypsophrys nicaraguense</i>		moga
	<i>Neetoplus nematopus</i>		moga
	<i>Parachromis dovii</i>	wolf cichlid	guapote
	<i>Parachromis loisellei</i>		guapotillo
	<i>Tomocichla underwoodi</i>	tuba	vieja
Mugilidae	<i>Agonostomus monticola</i>	mountain mullet	tepemechin
	<i>Joturus pichardi</i>	hog mullet	bobo
Gobiidae	<i>Awaous banana</i>	lamearena	lamearena
	<i>Sicydium adelum</i>	goby	chupapiedra
	<i>Sicydium altum</i>	goby	chupapiedra
Eleotridae	<i>Gobiomorus dormitor</i>	big-mouth sleeper	guavina
Fishes of the Río Sixaola sector			
Characidae	<i>Astyanax aenus</i> (= <i>A. fasciatus</i>)	banded tetra	sardina
	<i>Astyanax orthodus</i>	largespot	sardina blanca
Gymnotidae	<i>Gymnotus cylindricus</i>	knifefish	madre de barbudo
Rhamphichthyidae	<i>Hypopomus occidentalis</i>	knifefish	madre de barbudo
Pimelodidae	<i>Rhamdia guatemalensis</i>	catfish	barbudo
	<i>Rhamdia rogersi</i>	catfish	barbudo
Poeciliidae	<i>Alfaro cultratus</i>	alfaro	olomina
	<i>Brachyrhaphis parismina</i>	olomina	olomina
	<i>Phallichthys amates</i>	merry widow	olomina
	<i>Poecilia gillii</i>	molly	olomina
	<i>Priapichthys annectens</i>	olomina	olomina
Atherinidae	<i>Atherinella chagresi</i>	silverside	sardina
Syngnathidae	<i>Pseudophallus mindii</i>	pipefish	pez pipa
Synbranchidae	<i>Synbranchus marmoratus</i>	marbled swamp eel	anguila de pantano
Cichlidae	<i>Archocentrus myrnae</i>	topaz cichlid	mojarra
	<i>Archocentrus nigrofasciatus</i>	convict cichlid	congo
	<i>Astatheros bussingi</i>		mojarra
	<i>Astatheros rhytisma</i>		
	<i>Parachromis loisellei</i>		guapote amarillo
Haemulidae	<i>Pomadasys croco</i>	Atlantic grunt	roncador
Mugilidae	<i>Agonostomus monticola</i>	mountain mullet	tepemechin
	<i>Joturus pichardi</i>	hog mullet	bobo
Gobiidae	<i>Awaous banana</i>	lamearena	lamearena
	<i>Sicydium adelum</i>	goby	chupapiedra
	<i>Sicydium altum</i>	goby	chupapiedra
Eleotridae	<i>Gobiomorus dormitor</i>	big-mouth sleeper	guavina

to east, the Río San Carlos system and the Río Sarapiquí-Chirripó system (Bussing 1998). East of the Chirripó the rivers flow into the Caribbean, possibly an important difference in terms of the movement of fishes because fishes in the latter rivers must pass through intertidal, brackish, or marine waters to connect to other river systems. Interestingly, there do not appear to be significant differences between the fish fauna of these two types of rivers, although there are some. This may be because in the area around the city of Guápiles, numerous tributaries of the Río Chirripó (draining north to the Río San Juan) and the Tortuguero and Parismina systems (draining east into the Caribbean) are found within a few kilometers of each other. It is easy to imagine that one of the regular flooding events common to this area could move fishes between the north-draining systems and those that drain to the Caribbean.

To the east of Siquirres, from Matina to the port of Limón, as the topography flattens out into the coastal plain, there is a distinct lack of rivers. The only water now flowing through the seemingly endless banana plantations are tiny silt-filled streams. As one heads south, near Cahuita and down to the Panamanian border, there are smaller rivers that flow into the Caribbean and others that drain into the Sixaola system. This break is significant because there is a notable change in the fish communities between the Sixaola system and the northern part of the lowlands. The Río Sixaola and its tributaries have similar, related, but distinctly different species, than the rest of the region. For example, with regard to cichlids, although *Archocentrus septemfasciatus* is common throughout the entire northern quadrant, it is replaced in the Sixaola region by *Archocentrus myrnae* (Tobler 2007). Similarly, *Amphilophus alfari* is replaced by *Amphilophus bussingi*. This is not to say that no northern sector fish are found in the Sixaola. For example, although there is a different tetra, namely the largespot tetra, *Astyanax orthodus*, the banded tetra *A. aenus* is also there, as is the convict cichlid, which is found over much of northern Costa Rica (Bussing 1998).

Other species will be found once someone looks for them. For example, again with regard to cichlids, Bussing does not indicate *Neetroplus nematopus* in the Río San Juan, yet it is common both in the main part of the Caribbean lowlands and in Nicaragua. Other fishes, such as *Tomocichla underwoodi* (= *T. tuba*) are almost certainly not found in the Sixaola region because we have looked extensively for them and not found them there. Finally, there is the possibility that some fishes are located now where they have been introduced by humans. This is a common occurrence around the world both currently and historically and there is little reason to imagine that the Caribbean lowlands have been exempt from this influence.

The second key contrast between the Costa Rican Caribbean lowlands and the Amazon drainage concerns the changes in water volume and depth. The Amazonian flood cycle is present in the Costa Rican lowlands in almost similar magnitude, but is completely different in periodicity and tempo. The rivers of the main part of the Caribbean lowlands (there are no natural lakes as such, except for Lake Nicaragua on the northern boundary) are the product of constantly changing hydrodynamics. If anything, it is the variability that characterizes these habitats. The variation originates in the large-scale patterns of rainfall—heavy rains in late September through early January, the dry season from mid-January through April, the “little wet” season from May through August and then the “little dry” season through August and September. The timing of each of these periods changes from year to year. The important point is that even during the dry season, large storms can drop a substantial amount of water both on the lowlands and on the mountains to the west, which then rapidly moves down the streams and into the rivers. Rivers can swell in a matter of hours to twice their volume or more. For example, the height of the Río Puerto Viejo rose almost ten meters within 24 hrs at the La Selva Biological Station in January of 2006 and then dropped back to its original level over the next couple of days.

This variation in water volume can radically alter the physical environment, moving large woody debris tremendous distances and reshaping river substrates in minutes. The water itself also changes in temperature, dropping to near 20°C or lower, or rising up to 27°C or higher. With changes in water depth, areas that were slow-moving become rapids and vice versa. The rivers can flood huge areas of land, then recede, moving fish into places far from the original river. This is important because many of the fishes associate themselves with particular substrates, depths, and temperatures. While the physical conditions change, sometimes daily, so too does the distribution and activity of many of the fishes. In summary, although various species can be nominally placed as being native to the region, the exact location at which a species is found can vary daily. Almost two decades of underwater snorkel studies have revealed that just because a fish is found at a particular location today means little as to whether that species will be found there tomorrow or next week. An open question remains whether the fish move into and out of desirable portions of a river or whether they simply “hunker down” and wait out the bad weather. Clearly at least some fishes are moving large distances because stretches of some rivers will become disconnected or entirely dewatered during certain times of the year, yet have fishes at other times. Although *Rivulus* (a killifish) can occasionally be spotted “flipping” along the

ground from one body of water to the next, most of the fishes in the region are confined to living and dispersing in water.

A final key contrast with other aquatic environments is the almost complete lack of aquatic macrophytes in most of these rivers and streams. There simply are no plants in most places (see also Pringle et al., chapter 18 of this volume). The substrate is rock, gravel, sand, or compacted clay. The exception is during flooding events when terrestrial vegetation becomes inundated. Nor are there large-leaved aquatic or emergent plants on which the fish can lay eggs. Small fishes, such as many livebearers, persist by living along the margins of the rivers. Woody debris is critical for hiding, as well as for creating microclimates of different velocity, substrate, and temperature.

The taxonomy of some groups is a major challenge for understanding the fish communities of the Caribbean lowlands. For example, the convict cichlid, *Archocentrus nigrofasciatus*, has been placed in at least five genera within the last two decades (*Herichthys*, *Heros*, *Cichlasoma*, *Cryptoheros*, *Amatitlania*). These name changes reflect ongoing attempts to understand phylogenetic relationships that are not clearly resolved, largely because the biogeographic origins of these fishes are complicated (Chakrabarty and Albert 2011). Certainly some of the fishes are the result of radiations north from South America with the rise of the Isthmus of Panama, but the timing and numbers of these radiations are unclear. Other fishes have likely come from the north. The wolf cichlid (*Parachromis dovii*), or *guapote* as it is called locally, comes from a group with origins in the West Indies, yet the West Indian fishes are likely derived from older South American ancestors. No doubt further research will resolve some of these difficulties, particularly concerning closely related cichlid taxa such as *Poecilia gillii* and *P. mexicana*.

Research on fishes in the Caribbean lowlands has been hampered by several obstacles. The large amount of moving water and the large sediment load also mean that visibility varies from excellent to non-existent. Certain rivers, such as the Río Chirripó, have never had any appreciable visibility, and therefore our knowledge is limited to the results of sampling (fishing, electroshocking). Others, such as the Río Puerto Viejo or the Río San José, can range from almost clear to no visibility from one day to the next. Names of rivers in the region also pose a challenge in that names on maps do not always agree with names on road signs, with GIS systems, or with local names for a river. Also, certain names are used repeatedly for different rivers, even two rivers located relatively close to each other. For instance, Río Toro appears as the name of several rivers in the region and

there are two different rivers named Río Sardinal within 15 kilometers of each other, yet they are entirely unconnected. Similarly, different segments of a river often bear a different name. Finally, river connectedness is complex and may involve stream capture, reticulation, and intermittent flows. This complexity could be important for understanding the evolution and relatedness of populations and subpopulations of fishes.

The region and the fishes in it face various threats. Intense agriculture (particularly banana and pineapple) close to the rivers means that pesticides and sedimentation are always potential problems. Fishing by humans is present and likely responsible for local reduction in populations of some species—for example, *guapote* are increasingly rare and also wary of humans. *Tomocichla underwoodi* numbers near the town of Río Frio have decreased markedly over the last decade. Spear fishing, though illegal, is increasingly common and brazen and potentially a major threat because it specifically targets the largest individuals.

On January 8, 2009, a previously unrecognized threat demolished the Río Sarapiquí when a magnitude 6.1 earthquake on the Caribbean slope of Volcán Poas caused massive landslides of material into the headwaters and tributaries of the Río Sarapiquí. The main river channel became saturated with mud and debris such that it virtually solidified all the way down to the confluence with the Río Puerto Viejo (about 25 km). It appeared that most, possibly all, of the fish in the main river were killed at that time, apparently from oxygen deprivation. How frequently such events occur, and whether their magnitude is amplified by human effects on the terrain, is unknown.

On a positive note, the past decade has seen a notable increase in Costa Ricans using donning masks and snorkeling, simply to appreciate the beauty and environment of the lowland rivers. This is a positive development.

Amphibians

The lowland forests (below 300 m a.s.l.) of the Caribbean slope of Costa Rica host a diverse amphibian assemblage, with 91 species of frogs in 38 genera, 10 species of salamanders in two genera, and three species of caecilians in two genera (Table 16.2). Frogs are distributed among 14 families, yet salamanders and caecilians are each represented in the region by a single family. Of Costa Rica's 187 amphibian species, 104 occur in the Caribbean lowlands. There are no amphibian species that are endemic to the Caribbean lowlands of Costa Rica, largely because amphibian species in the lowland tropics generally have large geographic ranges (Savage 2002, Whitfield et al. in press). The amphibian fauna of the lowlands is quite distinct from

Table 16.2. (a) Diversity and Habitat Affiliations of Amphibians of the Caribbean Lowlands of Costa Rica

Taxon	Family	Genera	Species	Larval habitat	Adult habitat
Frogs	Rhinophrynidae	1	1	P	F
	Bufo	4	6	P,S	T
	Aromobatidae	1	1	S	T
	Dendrobatidae	5	5	S, Ph	T
	Eleutherodactylidae	1	2	D	A, T
	Brachycephalidae	1	17	D	A, Aq, T
	Strabomantidae	1	6	D	A, T
	Leiuperidae	1	1	P	T
	Leptodactylidae	1	4	P	F, T
	Amphignathodontidae	1	1	D	A
	Centrolenidae	3	11	S	A
	Hylidae	15	30	P, Ph, S	A
	Microhylidae	2	2	P	F
	Ranidae	1	4	P, S	Aq, T
	Salamanders	Plethodontidae	2	10	D
Caecilians	Caeciliidae	2	3	D	F
Total		42	104		

NOTE. Larval habitat indicates pond or pool breeding (P), stream-breeding (S), phytotelm-breeding (Ph), and direct-developing (D). Adult habitat indicates arboreal (A), aquatic (Aq), fossorial (F), or terrestrial (T).

Source: Data derived from Savage 2002 and IUCN 2006.

montane forests, but is rather similar to those amphibian faunas found from moist forests from southern Mexico through central Panama (Savage 2002). The amphibian fauna from the most intensively studied site in the region, La Selva Biological Station, hosts 55 species (52.9% of the Caribbean lowlands assemblage).

Three major ecological assemblages of amphibians found in Caribbean lowlands may be distinguished based primarily upon their use of reproductive resources: (1) lotic-breeding species with tadpoles in streams or rivers, (2) lentic-breeding species with larvae in ponds or pools, and (3) species with specialized forms of terrestrial reproduction. The stream-breeding assemblage is much less abundant and diverse in the lowlands than upslope, and in the lowlands glass frogs (Family Centrolenidae) are the most diverse representatives. The assemblage of lentic-breeding species may utilize habitats ranging from small forest pools to large permanent water bodies, and is particularly diverse in temporary wetlands (Donnelly and Guyer 1994). A few lentic-breeding species—including the dendrobatid *Oophaga pumilio* (previously *Dendrobates pumilio*) and the hylid *Cruziobyla calcarifer*—reproduce in phytotelmata. Terrestrial species with direct development (including the species-rich genera *Craugastor* and *Pritimatnis*) are particularly diverse and abundant in the Caribbean lowlands, likely because the high rainfall and lack of a severe dry season prevent terrestrial eggs from desiccating (Scott 1976, Whitfield et al. 2007).

Fortunately, for the most part, amphibian assemblages

in the lowland tropics have not been as severely affected by the rapid and devastating species loss occurring in montane sites (Lips et al. 2005, 2006, 2008, Whitfield et al. in press). Thirty-three percent of Costa Rican amphibians are listed by the IUCN as threatened with extinction, but only 22.1% of species in the Caribbean lowlands region are threatened, and these are mostly higher-elevation species whose ranges only marginally extend into the lowlands.

There are nonetheless many significant threats to lowland amphibian faunas, including widespread land-use change, emerging infectious diseases, and climate change (Butterfield 1994, Bell and Donnelly 2006, Whitfield et al. in press). The apparently non-native amphibian chytrid fungus, *Batrachochytrium dendrobatidis*, appears to be broadly distributed in this region and the neighboring volcanic cordilleras (Puschendorf et al. 2006, Puschendorf et al. 2009, and see Lawton et al., chapter 13 of this volume), but has not been reported to cause widespread declines here. However, at least one frog species (*Craugastor ranoides*) seems to have suffered extirpation throughout the region even close to sea level—possibly due to chytridiomycosis (Puschendorf et al. 2005, Puschendorf et al. 2006). Invasive competitors currently appear to represent little threat. Although at least one non-native frog has established small but persistent populations in this region (*Osteopilus septentrionalis* surrounding Puerto Limón), it is probably restricted to highly disturbed residential areas (Savage 2002). Whitfield et al. (2007) reported assemblage-wide declines for terrestrial frogs at La Selva, but the geographic extent and proximate

causes for these declines remain unclear. The most serious future threats to amphibian populations in addition to continued habitat loss will likely result from anthropogenic climate change, in particular if increases in temperature are accompanied by directional shifts in precipitation regimes (Aguilar et al. 2005, IPCC 2007, Lawler et al. 2009, Whitfield et al. in press).

Reptiles

The reptiles of the Caribbean lowlands of Costa Rica encompass a diverse assemblage including 36 species of lizards in 22 genera, 83 species of snakes in 47 genera, 6 species of turtles in 4 genera, and 2 species of crocodylians each in their own genus. In all, 127 of Costa Rica's 222 reptile species occur in the lowlands of the Caribbean versant. Over half of the diversity in this region belongs to colubrid snakes, but the anoles (Family Polychrotidae) constitute another conspicuously diverse group. Savage (2002) suggested that the reptile fauna of this region is composed of species forming a lowland moist forest assemblage that ranges from eastern Mexico through Panama and is differentiated from other Mesoamerican reptile assemblages occurring in upland or more xeric habitats. The reptile fauna of the most intensively studied site in the Caribbean lowlands, La Selva Biological Station, includes 89 species (70.0% of the regional pool; Guyer and Donnelly 2005).

The ecology of the reptiles is extremely variable, both within and among the major groups. The lizards in the region range from the large-bodied and primarily herbivorous *Iguana* to very small-bodied forest floor arthropod-eating lizards (*Lepidoblepharis*, *Norops*). A diverse assemblage of leaf-litter lizards includes anoles, geckos, teiids, gymnophthalmids, anguids, and skinks (Lieberman 1986). The anoles sort ecologically along a vertical gradient from leaf-litter to trunk-dwelling and canopy species (Irschick et al. 1997). The booid and viperid snakes are semi-arboreal (*Boa*), arboreal (*Corallus*, *Bothriechis*), or terrestrial (*Epicrates*, *Bothrops*, *Lachesis*, *Porthidium*) and feed primarily on vertebrates. The elapids feed mostly on other snakes. The highly diverse assemblage of colubrids ranges dramatically in body form and habitat preferences, with many arboreal, terrestrial, and fossorial species but relatively few aquatic species (Guyer and Donnelly 1990, 2005, Savage 2002). The colubrids also vary greatly in diet, preying upon arthropods (*Tantilla*), mollusks (*Dipsas*, *Sibon*), amphibians (*Chironius*, *Leptodeira*, *Leptophis*, *Urotheca*), lizards (*Scaphiodontophis*, *Imantodes*, *Oxybelis*), snakes (*Clelia*, *Drymarchon*, *Erythrolamprus*), birds (*Pseustes*), or mammals (*Lampropeltis*). The non-marine turtle fauna includes stream-dwelling species (*Rhinoclemmys funerea*, *Chelydra*, and *Trachemys*), pond-inhabiting species (two *Kinosternon*

and *Chelydra*), and a single terrestrial species (*Rhinoclemmys annulata*). The crocodylians include the spectacled caiman, *Caiman crocodilus*, which inhabits swamps, ponds, streams, and rivers, and the American crocodile, *Crocodylus acutus*, which occurs primarily in larger rivers.

The greatest threat to reptiles in the Caribbean lowlands is rampant habitat modification. Although some species of reptiles fare well in lands cleared of forests (especially heliothermic lizards such as *Ameiva* sp. and *Basiliscus vittatus*), most reptiles prefer intact forests. Turtles (particularly *Chelydra* and *Trachemys*) and green iguanas are hunted and consumed by humans. Crocodiles and caiman have been actively hunted by humans for meat and hides; and while crocodiles were extirpated through much of their range, conservation efforts have been extremely effective and crocodile populations have been recovering in the past two decades (Savage 2002). Three non-native species of lizards have established populations in the area (the house geckos *Hemidactylus frenatus* and *Hemidactylus garnotti*, and the Caribbean anole *Ctenopus cristatellus*) but appear to be confined to highly disturbed habitats and currently do not appear to pose a threat to native faunas. Huey et al. (2009) suggested that many forest-dwelling lizards are thermoconformers whose optimal body temperatures are low relative to ambient temperatures, and that human-induced increases in temperature are likely to have particularly adverse effects on these ectotherms in the near future.

Birds

The Atlantic lowland evergreen forests (below 300 m a.s.l.) along the Caribbean slope of Costa Rica are home to a highly diverse avifauna. These forests, as discussed earlier, are characterized by high rainfall, limited seasonality, a variety of habitat types, and complex vegetation structure within forests, all of which combine to support high bird species richness (Orians 1969, Slud 1976, Stiles 1983). These biotic and climatic factors ensure the availability of a wide variety of food resources such as fruits, flowers, nectar, and insects throughout the year, and also provide many unique resources for birds, such as army ant swarms (Blake and Loiselle 2000). The close proximity of the Caribbean slope, North America, and the once-continuous Caribbean forest belt connecting the region to the species-rich South American forests has further contributed to the origin of high species diversity in the Caribbean lowlands of Costa Rica, with species diversifying along elevational (e.g., golden-crowned and white-throated spadebills, *Platyrinchus coronatus* and *P. mystaceus*, respectively) and latitudinal (e.g., the northern and southern nightingale-wrens, *Microcerculus philometa* and *M. marginatus*, respectively) gradients (Levey and Stiles 1994). Finally, as with the birds

Table 16.3. (b) Diversity and Habitat Affiliations of Reptiles of the Caribbean Lowlands of Costa Rica

Taxon	Family	Genera	Species	Habitat
Lizards	Corytophanidae	2	3	A, T
	Iguanidae	2	2	A, T
	Polychrotidae	4	13	A, T
	Gekkonidae	5	7	A, T
	Teiidae	1	2	T
	Gymnophthalmidae	3	3	T
	Anguidae	2	3	T
	Scincidae	2	2	T
	Xantusiidae	1	1	T
	Snakes	Boidae	3	3
Ungaliophidae		1	1	A, T
Colubridae		37	69	A, Aq, F, T
Viperidae		5	7	A, T
Elapidae		1	3	F, T
Turtles	Chelydridae	1	1	Aq
	Kinosternidae	1	2	Aq, F
	Emydidae	2	3	Aq, T
Crocodilians	Alligatoridae	1	1	Aq
	Crocodylidae	1	1	Aq
Total		75	127	

NOTE. Habitat indicates arboreal (A), aquatic (Aq), fossorial (F), or terrestrial (T). Source: Data derived from Savage 2002.

of the Osa Peninsula (see Gilbert et al., chapter 12 of this volume), the birds of the Caribbean lowlands tend to have low population densities but high species packing, with co-occurring similar species segregating by prey type, foraging height, and substrate use, among other variables (Terborgh et al. 1990, Chapman and Rosenberg 1991).

As a result of these factors, the lowland Caribbean forests have the highest avian diversity in Costa Rica. A total of 484 species in 309 genera and 61 families has been recorded to date (Table 16.4). Of these, 289 are known or strongly suspected to breed in the Caribbean lowlands (Stiles and Skutch 1989, Garrigues and Dean 2007, Sigel et al. 2010). Yet, although the region hosts the highest species diversity, endemism rates are lower than on either the Osa Peninsula or the higher-elevation forests, likely due to the once-continuous extent of lowland forest from Mexico south into South America (Levey and Stiles 1994). The Costa Rican lowland Caribbean region hosts, during part to all of the year, 20 species that are endemic to southern Central America and northern Colombia. Of these, three species are also found in the Pacific lowlands and foothills of both coasts and 14 range into the Caribbean foothills. Four species—snowy cotinga (*Carpodectus nitidus*), plain-colored tanager (*Tangara inornata*), sulphur-rumped tanager (*Heterospingus rubrifrons*), and Nicaraguan seed-finch (*Oryzobus nuttingi*)—are restricted to the Caribbean lowlands, rarely ranging up to elevations above 700 m.

An additional 33 species of elevational migrants traverse

the Caribbean slope, presumably to track the availability of food resources. For example, the three-wattled bellbird (*Procnias tricarunculata*) and the resplendent quetzal (*Pharomachrus mocinno*) move downslope in the non-breeding season, following the availability of their preferred Lauraceae (avocado) fruits (Hamilton et al. 2003, Powell and Bjork 1994). However, one species of hummingbird—the violet-crowned woodnymph (*Thalurania colombica*)—reverses the trend by breeding in the lowlands and migrating upslope (Stiles and Skutch 1989). Elevational migrants are highly dependent upon forested habitat in both their breeding and non-breeding grounds, as well as along their migratory pathway, and perhaps as a consequence of forest loss and fragmentation, 27% of these species (9 of 33) are considered threatened (IUCN 2010).

Lowland Caribbean forests and disturbed areas (including secondary forests, open areas, and gardens) provide important overwintering habitat to many species of latitudinal migrants. Most latitudinal migrants breed in North America and either pass through Costa Rica on migration (76 species) or spend the non-breeding (winter) season in the lowland Caribbean area (49 species; Stiles and Skutch 1989, Parker et al. 1996, Garrigues and Dean 2007). These species have broader geographic ranges and are not as forest-dependent (and accordingly are not as threatened) as elevational migrants, with 7% of the species (9 of 125) considered threatened. The avifauna also includes three species of Austral migrants, which move annually between Costa Rica and South America. The streaked flycatcher (*Myiodynastes maculatus*) breeds in South America and spends the non-breeding season in the Costa Rican lowlands. An additional two species, the piratic flycatcher (*Legatus leucophaius*) and the yellow-green vireo (*Vireo flavoviridis*), breed in Costa Rica and migrate to South America during the late wet season (October–April).

The greatest avian diversity in the lowland Caribbean region is found in primary forests and older, tall secondary forests, with a total of 166 species. An additional 66 species are generalists, found in forests as well as in other habitats. Open areas, including fields, pastures, young second growth, gardens, and developed areas, have the next-highest diversity, with a total of 118 species. Edge habitats, between open and forested areas, are used by an additional 52 species. Finally, the region is home to 59 species using aquatic habitats (including lakes, rivers, and marshes), and 23 aerial species (mostly swallows and nightjars that spend the majority of their time on the wing; Sigel et al. 2010).

The avifauna takes advantage of the wide variety of food resources available within the lowland Caribbean forests throughout the year. Insectivores numerically dominate the lowland Caribbean region, with 167 species. Omnivores

are the second most-diverse dietary guild with 155 species, followed by carnivores with 97 species. The avifauna also includes 33 species of frugivores, 25 species of nectarivores, and 6 species of granivores.

One of the most notable features of tropical lowland avifauna, including that of the lowland Caribbean region of Costa Rica, is the single- and multispecies flocks. Five types of flocks are commonly found in lowland Caribbean forests: single species flocks, understory antwren/antvireo mixed flocks, understory-midstory tanager mixed flocks, canopy mixed flocks, and ant-followers. Thirty-two species of land-birds form single-species flocks, including the great green (*Ara ambiguus*) and scarlet (*A. macao*) macaws, chestnut-mandibled (*Ramphastos swainsonii*) and keel-billed (*R. sulfuratus*) toucans, and dusky-faced (*Mitrospingus cassinii*) and plain-colored (*Tangara inornata*) tanagers. Forest understory antwren-antvireo mixed flocks form around several nuclear species, including white-flanked (*Myrmotherula axillaris*), checker-throated (*Epinecrophylla fulviventris*), and dot-winged (*Microrhopias quixensis*) antwrens and streak-crowned antvireos (*Dysithamnus striaticeps*), which were among the most abundant understory species at La Selva in the 1970s, but are now scarce (Sigel et al. 2006). These flocks are attended by numerous species of wrens, gnatwrens, flycatchers, and woodcreepers, including the sulphur-rumped flycatcher (*Myiobius sulphureipygius*), buff-throated foliage-gleaner (*Automolus ochrolaemus*), and plain xenops (*Xenops minutus*). Tanager flocks form around two nuclear species, tawny-crested (*Tachyphonus delatirii*) and olive (*Chlorothraupis carmioli*) tanagers, and are attended by many species of tanagers, finches, flycatchers, and woodcreepers, including the yellow-margined flycatcher (*Tolmomyias assimilis*), the white-throated shrike-tanager (*Lanio leucothorax*), and the orange-billed sparrow (*Arremon aurantirostris*). Canopy mixed flocks include cacique flocks formed around the scarlet-rumped cacique (*Cacicus uropygialis*), greenlet-honeycreeper flocks formed around the lesser greenlet (*Hylophilus decurtatus*) and the shining honeycreeper (*Cyanerpes lucidus*), and grosbeak flocks centered around the nuclear species black-faced grosbeak (*Caryothraustes polioaster*); the latter two canopy flocks are frequently attended by Nearctic migrant warblers as well as resident species. Finally, ant-following flocks form around three nuclear species: bicolored (*Gymnopithys leucaspis*), ocellated (*Phaenostictus mcleannani*), and spotted antbirds (*Hylophylax naevioides*). These flocks are joined by several obligate and facultative attendant species, including northern barred-woodcreeper (*Dendrocolaptes sanctithomae*), plain-brown woodcreeper (*Dendrocincla fuliginosa*), bare-crowned (*Gymnocichla nudiceps*) and immaculate (*Myrmeciza immaculata*) antbirds, red-throated

ant-tanagers (*Habia fuscicauda*), and rarely the rufous-vented ground-cuckoo (*Neomorphus geoffroyi*).

The lowland Caribbean avifauna faces a wide variety of threats, including global climate change (Clark et al. 2003, Colwell et al. 2008), pesticides (Matlock et al. 2002), and cascading effects of alterations to other components of the lowland rainforest community (Feeley and Terborgh 2008, Young et al. 2008, Michel 2012). However, the greatest threat is the loss and fragmentation of lowland evergreen forests. Forested land cover in the Caribbean lowlands has decreased from nearly 100% to 70% in 1963 to 35% by 1983, and forest loss has continued since this time (Read et al. 2001). As a result, a total of 55 species are considered near-threatened, threatened, or vulnerable according to the IUCN (2010), and/or of medium, high, or urgent conservation priority (Parker et al. 1996). The majority of these species (36, or 65%) are associated with forest habitats, and another 5 species of generalists spend some time in forested habitats.

Fragmentation-associated threats to lowland Caribbean forest birds also disproportionately affect species of various dietary guilds, specifically insectivores. Although the distribution of threatened species amongst dietary guilds of all species in all habitats in the lowland Caribbean is relatively even (8 carnivores, 14 frugivores, 3 granivores, 14 insectivores, 3 nectarivores, and 13 omnivores), understory insectivores have been particularly hard hit at the La Selva Biological Station in the Sarapiquí region. At La Selva, 51 species have experienced moderate or severe declines since 1960, including 8 species that are believed extirpated. Of these, 65% (33 of 51) are insectivores, 41% (21 of 51) are ant-followers or associated with mixed flocks, and 47% (24 of 51) are residents of the forest understory. The nuclear species of both the antwren-antvireo understory mixed flocks (*M. axillaris*, *E. fulviventris*, and *M. quixensis*) and the tanager mixed flocks (*T. delatirii* and *C. carmioli*) are among the species that have experienced declines at La Selva, which in turn has apparently led to declines of attendant species, including the sulphur-rumped flycatcher (*M. sulphureipygius*) and white-throated shrike-tanager (*L. leucothorax*; Sigel et al. 2006). It has not yet been established with certainty whether the trends seen at La Selva are widespread throughout the Caribbean lowlands. In any case, insectivore declines have important implications for arthropod and plant communities, as insectivorous birds (along with bats) at La Selva protect plants by consuming herbivorous arthropods (Michel et al. 2014).

Mammals

Costa Rica is one of the few countries in the Western Hemisphere in which the entire mammalian fauna that was present

Table 16.4. Diversity, Migratory Status, Habitat Guilds, Dietary Guilds, and Number of Threatened Species among Birds of the Caribbean Lowlands of Costa Rica

Family	Genera / species	Permanent residents ^a	Latitudinal migrants ^b	Elevational migrants ^c	Visitants ^d	Habitat guilds ^e	Dietary guilds ^f	Threatened species ^g
Tinamidae	2/3	3	0	0	0	F, O	O	1
Anatidae	5/6	2	3	0	1	Aq	O	0
Cracidae	3/3	2	0	0	1	F	O	2
Odontophoridae	2/3	2	0	0	1	F	O	2
Podicipedidae	2/2	2	0	0	0	Aq	C	0
Phalacrocoracidae	1/1	1	0	0	0	Aq	C	0
Anhinga	1/1	1	0	0	0	Aq	C	0
Ardeidae	11/17	11	6	0	0	Aq, F, O	C, I	1
Threskiornithidae	4/4	2	0	0	2	Aq, F	C	0
Ciconiidae	1/1	0	0	0	1	Aq	C	0
Cathartidae	3/3	3	0	0	0	F, O	C	0
Accipitridae	19/33	19	11	1	2	Ae, Aq, E, F, G, O	C, I	6
Falconidae	5/10	6	3	0	1	E, F, O	C	1
Rallidae	8/9	6	2	0	1	Aq, F	O	1
Heliornithidae	1/1	1	0	0	0	Aq	O	0
Eurypygia	1/1	1	0	0	0	F	C	0
Aramidae	1/1	0	0	0	1	Aq	C	0
Charadriidae	3/3	0	2	0	1	Aq	I	0
Recurvirostridae	1/1	0	1	0	0	Aq	C	0
Jacaniidae	1/1	0	1	0	0	Aq	O	0
Scolopacidae	6/13	0	13	0	0	Aq, O	C, I	1
Columbidae	7/14	11	0	0	3	F, O	E, F, O	2
Psittacidae	8/12	9	0	3	0	E, F, G, O	F	6
Cuculidae	5/8	4	3	0	1	F, G, O	C, I, O	1
Tytonidae	1/1	1	0	0	0	O	C	0
Strigidae	6/7	7	0	0	0	F, G, O	C, I	0
Caprimulgidae	4/7	4	3	0	0	Ae, F, O	I	0
Nyctibiidae	1/2	2	0	0	0	F, O	C, I	0
Apodidae	4/8	3	1	0	4	Ae	I	1
Trochilidae	21/26	12	1	8	5	E, F, G, O	N	3
Trogonidae	1/5	3	0	2	0	F	O	0
Momotidae	3/3	2	0	0	1	F, G	O	0
Alcedinidae	2/6	5	1	0	0	Aq, F	C	0
Bucconidae	3/4	4	0	0	0	E, F, G	I	0
Galbulidae	2/2	2	0	0	0	E, F	I	0
Ramphastidae	4/5	3	0	2	0	F, G	O	2
Picidae	7/9	8	1	0	0	E, F, G, O	I, O	1
Furnariidae	11/14	12	0	0	2	F, G, O	I	1
Thamnophilidae	13/18	16	0	2	0	E, F, O	I	3
Formicariidae	1/1	1	0	0	0	F	I	0

continued

at the time of European settlement is still largely extant, at least in well-protected parks. The Caribbean lowland area of Costa Rica has a diverse mammalian fauna that is characteristic of Neotropical lowland rain forests and consists of approximately 125 species representing 10 orders and 30 families. The majority of species found in the lowlands are broadly distributed in the northern Neotropics—lowland tropical mammals tend to be distributed both in latitude and elevation in a manner more widespread than is the case for amphibians, reptiles, and birds.

The Costa Rican Caribbean lowland mammal fauna includes 5 marsupials, 71 (possibly more) bats, 3 (possibly 4) primates, 2 armadillos, 3 anteaters, 1 rabbit, 3 squirrels, 10 (possibly more) long-tailed rats and mice, 1 pocket gopher,

1 porcupine, 1 paca, 1 agouti, 4 mustelids, 1 skunk, 4 procyonids, 5 cats, 2 peccaries, 2 deer, and 1 tapir. The West Indian manatee (*Trichechus manatus*) historically occurred in the rivers and canals along and well inland from the coast and it is still found there now, although in reduced numbers (Jiménez, chapter 20 of this volume). This species list is likely to be complete with the exception of the orders Chiroptera and Rodentia, where cryptic or difficult-to-capture species may not yet have been observed. All of the species in this historical species list, with the exception of the giant anteater (*Myrmecophaga tridactyla*), still occur in the lowlands and represent more than half (55%) of Costa Rica's mammalian fauna.

Although Costa Rica's Caribbean lowlands occupy an

Table 16.4. Continued

Family	Genera / species	Permanent residents ^a	Latitudinal migrants ^b	Elevational migrants ^c	Visitants ^d	Habitat guilds ^e	Dietary guilds ^f	Threatened species ^g
Grallariidae	1/2	2	0	0	0	E, F	I	0
Tyrannidae	36/54	35	13	3	3	E, F, G, O	F, I, O	3
Cotingidae	5/5	2	0	2	1	F	F, O	3
Pipridae	3/4	1	0	3	0	E, F	F	1
Vireonidae	3/10	3	7	0	0	E, F, G, O	I, O	0
Corvidae	1/2	2	0	0	0	G, O	O	0
Hirundinidae	6/9	3	6	0	0	Ae, O	I	0
Troglodytidae	6/10	10	0	0	0	E, F, O	I	1
Sylviidae	3/3	3	0	0	0	E, F, G	I	0
Turdidae	4/8	1	4	2	1	F, G, O	O	1
Mimidae	2/2	1	1	0	0	E, O	O	0
Bombycillidae	1/1	0	1	0	0	G	O	0
Parulidae	13/34	3	31	0	0	E, F, G, O	I, O	3
Genus Incertae Sedis (Coerebidae)	1/1	1	0	0	0	O	O	0
Thraupidae	14/27	17	3	3	4	E, F, G, O	I, O	3
Genus Incertae Sedis (Saltator)	1/5	5	0	0	0	E, F, O	O	1
Emberizidae	8/11	8	2	0	1	F, O	G, O	2
Cardinalidae	5/7	2	4	1	0	F, G, O	G, O	1
Icteridae	9/15	12	3	0	0	E, F, G, O	I, O	0
Fringillidae	1/4	3	0	1	0	G, O	F	1
Passeridae	1/1	1	0	0	0	O	O	0
Total	309/484	286	128	33	37			55

^a Permanent residents live in the lowland Caribbean year-round.

^b Latitudinal migrants include passage migrants and breeding and non-breeding part-year residents that spend the remainder of the year in North or South America.

^c Elevational migrants include breeding and non-breeding part-year residents that spend the remainder of the year at higher elevations.

^d Visitants occur accidentally or visit occasionally, though not on a seasonal or annual basis.

^e Habitat guild codes: Ae: Aerial (spend most time on the wing); Aq: Aquatic (associated with lakes, rivers, and marshes); E: edge (associated with forest edge and canopy); F: Forest (associated with primary or tall secondary forest); G: Generalist (associated with multiple habitat types); O: Open (associated with fields, pastures, young secondary forest, suburban, and urban areas). Codes from Sigel et al. 2010.

^f Dietary guild codes: C: Carnivores (diet primarily or entirely vertebrates, carrion, snails, and large arthropods); F: Frugivores (diet primarily or entirely fruit); G: Granivores (diet primarily or entirely seeds); I: Insectivores (diet primarily or entirely insects and other arthropods); N: nectarivores (diet primarily or entirely floral nectar); O: Omnivore (diet includes food from multiple categories). Codes from Sigel et al. 2010.

^g Threatened species include species assigned Conservation Priority of Urgent (1), High (2), or Medium (3) by Parker et al. 1996 (per Blake and Loiselle 2000), and/or species assigned an IUCN (2010) Red List Category of Near Threatened or higher.

Source: Data derived from Slud 1960, Stiles and Skutch 1989, Ridgely and Gwynne 1992, Parker et al. 1996, Blake and Loiselle 2000, Sigel et al. 2006, 2010, Garri-gues and Dean 2007, and IUCN 2010.

extensive area from the Nicaraguan to Panamanian borders, until recently little research has been undertaken on the region's mammals other than in the La Selva–Parque Nacional Braulio Carrillo region and to a lesser extent in the Maquenque and Tortuguero protected areas. More than 100 scientific papers on various aspects of mammals at La Selva have been published since Slud (1960) first mentioned white-lipped peccaries, monkeys, and tapirs there. As part of the elevational transect that became the La Selva–Parque Nacional Braulio Carrillo biological corridor, Timm et al. (1989) conducted a faunal survey of the elevational transect from 35 m to 2,600 m on Volcán Barva, documenting that at least 141 species of mammals occurred in the protected area. They reviewed the historical and present-day distributions, systematics, and ecology of each species. This

research was the first such elevational transect undertaken in the Neotropics.

Three species of primates inhabit the Caribbean lowlands of Costa Rica, the mantled howler monkey, Central American spider monkey, and white-faced capuchin monkey. All three species were widely distributed throughout the Caribbean lowlands historically. During the early 1950s, primate populations throughout Central America were ravaged by an epidemic of mosquito-borne yellow fever (Fishkind and Sussman 1987, Timm 1994). Primates were observed only infrequently at La Selva between the late 1960s and early 1980s. Fortunately, all three species rebounded and they became more abundant than they were in the 1960s and late 1970s. Today capuchin, howler, and spider monkeys can be seen almost daily in protected areas and nearby for-

est fragments, often in large groups. Capuchin and howler monkeys can occupy quite small fragments, moving along fencerows. Capuchins living in close proximity to banana plantations feed on ripe bananas from the plantations. Historically, howler monkeys were the most abundant primates in the Caribbean lowlands, and this still may be the case today. A sighting of the night monkey (*Aotus*) at La Selva has never been confirmed or repeated.

The order Carnivora deserves special mention, not because there have been many studies on these animals, but because of their critical role in ecosystems (Terborgh 1988) and because they represent some of the animals most sought after by researchers and visitors alike. The most commonly seen species of the Carnivora are actually omnivorous or frugivorous—the white-nosed coati (*Nasua narica*), kinkajou (*Potos flavus*), and tayra (*Eira barbara*). The northern raccoon (*Procyon lotor*) occurs in low density in this area, which is interesting given its extremely wide distribution from southern Canada to central Panama and its high abundance in other areas of its range. The Neotropical otter (*Lontra longicaudis*) can be seen along streams and its fecal remains of fish and crustacean debris can be found on rocks. The ocelot (*Leopardus pardalis*) is the most frequently seen of the cats; it adapts well to disturbed habitats and can be found in small fragments, although little is known about how these populations are affected by fragmentation and the development of roads. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the two large cats found in the area. The jaguar is now extremely rare, especially in the lowlands, although wandering individuals are occasionally seen. The puma, on the other hand, although not abundant, is more common than the jaguar and is seen regularly at La Selva. Given the number of observations in recent years in many areas of the country, it appears as if puma numbers are increasing. The majority of sightings at La Selva are in areas where collared peccaries are frequently observed. Most of the data collected on felines in the Caribbean lowlands come from camera-trapping efforts by TEAM (the Tropical Ecology Assessment and Monitoring project of Conservation International, CI), a long-term biodiversity monitoring program that has been successful in capturing pictures of elusive animals from the lowlands (Ahumada et al. 2011). The coyote (*Canis latrans*), a generalist predator, recently expanded its range in Costa Rica to include the Caribbean lowlands.

Costa Rica has a rich and diverse bat fauna with all of the families and feeding niches found in the New World represented. There are currently 117 species of bats known from the country, which means that more than 50% of Costa Rica's terrestrial mammals are bats. The middle and higher elevation slopes have received far less study than

have the lowlands. The Caribbean lowland zone has a fauna of at least 71 bat species that includes all of the Neotropical families and most of the genera, as well as all of the feeding niches. More research has been undertaken on bats in the Caribbean lowlands than has been undertaken on all other Costa Rican mammals combined throughout all of the country. La Selva, with its rich bat fauna and ready access to both mature forest and varying stages of second growth, has been the center of bat research in Costa Rica for nearly five decades. The Tirimbina Biological Reserve has also become an important center of bat research in the past decade.

Early studies on bats at La Selva focused primarily on distributions, basic ecology, and systematics, providing a background for in-depth studies of behavior and ecology, as well as for assessing recent changes in distribution and abundance. LaVal (1977) reported on the distribution of several then poorly known species that he found at La Selva, including the first records of the thumbless bat (*Furipterus horrens*). Inexplicably, this species has never again been detected in Costa Rica despite the intensive netting and acoustical monitoring efforts in the lowlands. Critical to later studies on ecology and conservation of bats has been the presence of voucher specimens that the early researchers deposited in scientific collections and detailed keys for the identification of species, which were based heavily upon studies undertaken at La Selva (Timm and LaVal 1998, Timm et al. 1999).

When the white tent-making bat (*Ectophylla alba*) was discovered at La Selva, it was considered one of the rarest of New World bats and little was known of its biology (Timm 1982). Research has been undertaken on this species over several decades there and at Tirimbina, documenting that it alters the shape of *Heliconia* leaves by cutting the midrib along the length of the leaf, causing the sides of the leaf to collapse down around the bats and forming a roost site that protects the bats from predators as well as acting as a rain shield. Research on the tent-making bat species (including *Dermanura phaeotis*, *D. watsoni*, *Uroderma bilobatum*, *Vampyressa thuyone*) has provided several exciting new insights into bat biology (LaVal and Rodríguez-Herrera 2002, Rodríguez-Herrera et al. 2007, 2008, Rodríguez-Herrera and Tschapka 1999, Timm 1982, 1984, 1985, 1987).

Numerous other studies with nectar-feeding bats (Greiner et al. 2013, Sperr et al. 2009, Tschapka 2003, Voigt 2004, 2013), sac-winged bats (Voigt 2005, Voigt et al. 2008), vampire bats (Voigt et al. 2012), and others make this group of lowland Caribbean vertebrates one of the best studied in all of the New World tropics.

There have been few ecological studies on rodents in the Caribbean lowlands almost certainly because most species

are found in low numbers and are difficult to capture. The most recent ecological study was on the vesper mouse, *Nyctomys sumichrasti* (Rodentia: Cricetidae), a poorly known, arboreal, nocturnal species found throughout much of Central America. Romero and Timm (2013) documented that vesper mice have 1:1 sex ratios, they reproduce year-round, and litters may occur in rapid succession. Litter size is small with a mode of two, and embryos are not evenly distributed across the uterine horns contrary to hypotheses predicting that arboreal species would balance weight distribution.

In a recent synthesis of group dynamics, behavior, and current and historical abundances of peccaries in the Caribbean lowlands, Romero et al. (2013) documented that collared peccaries were historically found in quite low numbers, whereas white-lipped peccaries were abundant being found in large herds throughout the region. During the 1960s white-lipped peccaries declined, and are now extirpated from most of the lowlands. On the other hand, beginning in the late 1970s, collared peccaries increased in numbers and are now abundant at La Selva, where they are protected. Collared peccaries do not exhibit a habitat preference between primary and secondary forests, although they may behave differently in the two forest types.

Plant–Animal Interactions

Interactions between plants and animals have profound impacts on ecosystem attributes. Here we focus on two particular types of interactions—herbivory and seed dispersal.

Herbivory Rates in Caribbean Lowland Forests

Summarizing the complex theoretical framework of plant–herbivore interactions goes beyond the scope of this chapter (for three excellent reviews of this topic see Barone and Coley 2002; Coley and Barone 1996; Marquis and Braker 1994). However, it is important to note that many of the studies conducted in the Caribbean lowlands of Costa Rica represent part of the foundations of current herbivory theories.

Most of the biomass in tropical rain forests is concentrated in the canopy (Rinker and Lowman 2001) and, therefore, most of the interactions between plants and their herbivores (in absolute terms) would be expected to occur in the upper strata of the forest (Lowman 1995, Rinker and Lowman 2001). In the canopy, however, leaves fully exposed to the sun suffer significantly lower herbivory rates than do leaves in the shade; research in tropical rain forests in Australia and Panama suggests that herbivory rates are higher in understory plants than in the forest canopy (Lowman 1995).

In mature moist tropical forests, it has been estimated

that understory vegetation contains only about 3% of the aboveground biomass (Clark et al. 2001). The available estimates of herbivory rates in the Caribbean lowland forest of Costa Rica, however, are mostly for understory plant species so the comparison between canopy and understory herbivory for these forests cannot be made at this time. Two community-level studies at La Selva (one including 77 plant species and the other covering 45 species) revealed herbivory rates of 12.4% and 8.6%, respectively (Marquis and Braker 1994). These estimates are within the 7.0%–20.3% average herbivory estimates for other tropical rain forests understories, and are higher than the herbivory rates reported for temperate forests (Marquis and Braker 1994).

Herbivory by Vertebrates

A study performed in the Sábalo creek, a fourth-order stream bordering La Selva Biological Station, found that most of the fish species are herbivores. Non-planktonic plant matter represented more than 25% of the diet of 77% of the species (Wootton and Oemke 1992). Fish species including more than 50% of plant matter in their diets include *Astyanax fasciatus*, *Brycon guatemalensis*, *Bryconamericus scleroparius*, *Melaneris chagresi* (Characidae), *Cichlasoma tuba*, *C. alfari*, *C. septemfasciatum*, *C. nigrofasciatum*, *C. nicaraguense* (Cichlidae), and *Neoheterandria umbratilis* (Poeciliidae) (Wootton and Oemke 1992).

In the canopy, the largest and most conspicuous lizard is the green iguana (*Iguana iguana*). Juvenile green iguanas feed on both leaves and arthropods (Hirth 1963). Adults are mostly herbivorous, feeding on leaves, flowers, and fruits (Guyer and Donnelly 2005). In the understory, two folivorous turtles are present—the brown wood turtle (*Rhinoclemmys annulata*) and the black wood turtle (*Rhinoclemmys funerea*). The diets of both species include more than 50% of plant tissue (Guyer and Donnelly 2005). The brown wood turtle feeds on vines, shrubs, and ferns in the forest understory, and the black wood turtle forages terrestrially along river edges, usually at night (Acuña-Mesén 1998, Guyer and Donnelly 2005, and see Pringle et al., chapter 18 of this volume).

In tropical rain forests, the biomass of folivorous mammals is 1.5 to 5 times higher in the canopy than in the understory (Leigh 1999). This is not surprising, as most of the annual net production of vegetation in tropical rain forests is concentrated in the forest canopy (Clark et al. 2001, Lowman 1995). Four predominantly folivorous mammal species are found in the canopies of Caribbean lowland forests: the howler monkey (*Alouatta palliata*), the brown-throated three-toed sloth (*Bradypus variegatus*), Hoffmann's two-toed sloth (*Choloepus hoffmanni*), and the Mexican hairy porcupine (*Coendou mexicanus*). The diets of these four

species are composed of more than 50% leaf tissue. Other canopy dwellers are the Central American spider monkey (*Ateles geoffroyi*) and the white-headed capuchin monkey (*Cebus capucinus*). These two species are mostly frugivorous; however, they complement their diets with leaves (Marquis and Braker 1994). In the understory, five mammal species are the predominant folivores—the forest rabbit (*Sylvilagus brasiliensis*), the collared peccary (*Pecari tajacu*), the white-tailed deer (*Odocoileus virginianus*), the Central American red brocket (*Mazama temama*, formerly *M. americana*), and the locally rare Baird's tapir (*Tapirus bairdii*). The white-lipped peccary (*Tayassu pecari*), a primarily herbivorous mammal that once inhabited the Caribbean lowland of Costa Rica, almost has been extirpated (Romero et al. 2013).

Herbivory by Invertebrates

Insects are the most important herbivores in the tropical rain forest. In addition to the outstanding species diversity of this group, insect herbivores contribute to most of the herbivory in both canopy and understory plants (Lowman 1995, Rinker and Lowman 2001). One example of this high diversity is the insect community at La Selva. At least 171 families of phytophagous insects are present in this forest alone (Coley and Barone 1996). Most of these insects have specialized diets, feeding on one or a few plant species (Dyer et al. 2007, García-Robledo and Horvitz 2011, 2012a,b). In this section we discuss some aspects of the natural history for the main insect herbivore guilds, and also some plant-herbivore associations that have been thoroughly studied in the Caribbean lowlands.

In Costa Rica's Caribbean lowland forests, most associations between plants and sap-feeders remain unknown. A study on the distribution of cast nymphal skins of the sundown cicada (*Fidicina mannifera*, Homoptera: Cicadidae) suggests a potential association between this insect and plants from the family Fabaceae (Young 1980, 1984). Another large homopteran found in the region, the peanut-head bug (*Fulgora laternaria*, Homoptera: Fulgoridae) feeds on the sap of *Simarouba amara* (Simaroubaceae) (Orlando Vargas, personal observation). In the Caribbean lowlands, treehoppers are apparently generalists, feeding on a wide range of host plants (Wood 1993).

Leaf-miners are endophytic herbivores that feed within the tissue of leaves during larval stages. The orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera include leaf-mining species. Tropical leaf-miners have very restricted diets, with most species being monophagous. At La Selva, 130 species of leaf-mining beetles (71 Buprestidae, 41 Hispinae, 18 Curculionidae) were recorded (Hespenheide 1985, 1991). Most leaf-mining species consume a very

small fraction of the leaf tissue of their host plants, and it is suggested that herbivory by leaf-miners does not represent a significant contribution to the total herbivory in tropical rain forests.

Leaf-cutter ants are the predominant herbivores in the neotropics (Perfecto and Vandermeer 1993). It is estimated that leaf-cutting ants consume between 12 and 17% of the total leaf production (Cherrett 1986, Haines 1978, Wirth et al. 1997). In the Caribbean lowlands, the leaf-cutting ant *Atta cephalotes* is a common herbivore in agricultural areas, secondary forests, and old-growth forests (Perfecto and Vandermeer 1993). During the past years scientists have been working on research topics such as the symbiotic interactions among leaf-cutting ants, basidiomycete fungi, and nitrogen-fixing bacteria (Pinto-Tomas et al. 2009); the chemical ecology of plant-*Atta* interactions (Nichols-Orians 1991a,b,c,d); and foraging strategies, demography, and leaf-cutting ants' effects on soil changes, seedling recruitment, and forest regeneration (Farji-Brener 2001, 2005, Farji-Brener et al. 2010, Farji-Brener and Illes 2000, Folgarait et al. 1996, Peñaloza and Farji-Brener 2003).

The ecology of Neotropical acridid grasshoppers (families Acrididae and Romaleidae) is best known from species in the Caribbean lowlands as the result of extensive research on this group at La Selva (Braker 1986, 1989a,b, 1991, 1993, Rowell 1978, 1983a,b,c,d, 1985a,b). Although most temperate species of acridid grasshoppers are generalists, in neotropical rain forests they can display diet breadths that range from strict specialization to one host plant to generalist diets (Marquis and Braker 1994). For example, at La Selva, one species of grasshopper from the subfamily Copiocerinae feeds only on geonoid and bactroid palms (Marquis and Braker 1994). In contrast, the grasshopper *Microtylopteryx hebari* (Subfamily Ommatolampinae) feeds on at least 60 species of plants in 17 monocotyledonous and dicotyledonous families (Braker 1986, 1991). In the Caribbean lowlands, grasshoppers from the subfamily Proctolabinae are mostly specialists, feeding on plants from the families Nyctaginaceae and Solanaceae. Grasshoppers from the subfamily Ommatolampinae and the family Romaleidae usually have broader diets (Marquis and Braker 1994).

Lepidopteran larvae are an important component of insect herbivore communities in tropical rain forests. In some forests, caterpillars may account for more than 95% of the total number of species, number of individuals, and biomass of externally feeding holometabolous larvae (Novotný and Basset 2000, Novotný et al. 2002). In the Caribbean lowland forests of Costa Rica, larval lepidopterans are known to have a strong impact on seedling recruitment (Dyer et al. 2010).

In the Caribbean lowlands, herbivory rates by Lepidop-

tera are known for understory shrubs of the genus *Piper* (Piperaceae). In a study performed in four Caribbean forests (Bijagual, El Bejuco, and Tirimbina Biological Reserve, and Parque Nacional Braulio Carrillo), the average amount of herbivory attributed to lepidopterans on new leaves of *Piper* shrubs is 82.3% (Dyer et al. 2010).

The lepidopteran fauna in the Caribbean lowland forest of Costa Rica has been thoroughly studied in comparison to other Neotropical forests. Two long-term projects have generated comprehensive inventories for adult butterflies at La Selva and in Braulio Carrillo (i.e., the Arthropods of La Selva Project [ALAS] and the Tropical Ecology Assessment and Monitoring Network–Costa Rica [TEAM project–Volcán Barva]). In the Sarapiquí area, the associations of caterpillars and their host plants are known for 3,028 lepidopteran species and morphospecies (Gentry and Dyer 2002). Caterpillars at La Selva are associated with at least 307 host plant species (Dyer and Gentry 2002).

The genus *Piper* (Family Piperaceae) is a diverse pantropical genus of shrubs, vines, and small trees (Dyer and Palmer 2004). One third of the ca. 1,000 described species of *Piper* are Neotropical in distribution (Dyer and Palmer 2004). In the Caribbean lowlands of Costa Rica, plants in the genus *Piper* have been the focus of several remarkable studies on plant–herbivore interactions. Studies of plant–herbivore interactions with *Piper trigonum* (formerly known as *Piper arieianum*) represent the initial evidence that in a tropical plant, resistance against herbivore attacks has a genetic basis and an impact on life history traits such as growth, seed production, and seed viability (Marquis 1984, 1990, 1992).

Current research on *Piper*–arthropod interactions in the Caribbean lowland forests of Costa Rica includes topics such as the chemical ecology of plant–herbivore interactions and the direct and indirect effects of trophic networks on herbivory rates (Dyer and Palmer 2004). At present, the genus *Piper* is considered to be an emerging model system to understand evolutionary and ecological processes in plant–animal interactions (Dyer and Palmer 2004). The insect herbivore fauna of *Piper* in the Caribbean lowland forests of Costa Rica is diverse. Specialist herbivores include geometrid moths (*Eois* spp. and *Epimecis* sp.), skippers (e.g., *Quadrus cerealis*), and stem borer weevils from the genus *Ambates*. Specialist flea beetles (genus *Physimera*) feed on leaf tissue. Generalist folivores include apatelodid, limacodid, and saturniid moths. Herbivory by leaf-cutting ants and orthopterans is also common (Dyer and Palmer 2004).

The association between plants from the order Zingiberales and beetles from the genus *Cephaloleia* (Chrysomelidae: Cassidinae) is one of the oldest and most conservative plant–herbivore interactions (García-Robledo and Staines 2008, Wilf et al. 2000). In the literature, *Cephaloleia* beetles

are frequently included in a non-monophyletic group known as the “rolled leaf” beetles, because adults feed and mate in the scrolls formed by the young leaves of their host plants (García-Robledo and Horvitz 2011, 2012a).

In the Caribbean lowlands of Costa Rica, associations between *Cephaloleia* and their host plants have been investigated over the past three decades (García-Robledo and Horvitz 2012b). Research on the genus *Cephaloleia* includes the use of plant chemical signals for the location of host plants (García-Robledo and Horvitz 2009), the effects of plant chemical defenses and nutrient contents on insect performance (Auerbach and Strong 1981, Gage and Strong 1981), population dynamics (Johnson 2004a,b, Johnson 2005, Johnson and Horvitz 2005, Morrison and Strong 1981) and the structure of *Cephaloleia* species assemblages (Strong 1981, Strong 1982a,b). *Cephaloleia* species are also model organisms used to understand plant–herbivore evolutionary processes and the diversification of tropical insect herbivores (García-Robledo and Staines 2008, McKenna and Farrell 2005, 2006, Strong and Wang 1977, Wilf et al. 2000).

The species composition and diet breadth of *Cephaloleia* beetles is particularly well known for La Selva (García-Robledo et al. 2013). In this forest, at least 40 species of *Cephaloleia* are known to associate with at least 43 native plants from the order Zingiberales (García-Robledo 2010, Staines 1996). Diet breadths of *Cephaloleia* species at La Selva range from strict monophagous, such as *Cephaloleia fenestrata* which feeds only on *Pleiostachya pruinosa* (Marantaceae), to generalist species, such as *Cephaloleia belti*, which feeds on 15 plant species from three families of Zingiberales (García-Robledo and Horvitz 2009, 2011, 2012a).

Frugivory and Seed Dispersal

More than 90% of the woody plant species in a Caribbean lowland forest in Costa Rica have seeds adapted for dispersal by animals (Chazdon et al. 2003). Animals disperse seeds via endozoochory (defecation or regurgitation of intact, ingested seeds), ectozoochory (expectoration or dropping of seeds carried externally by a disperser), or hoarding (burial of seeds in subsurface caches). Dispersed seeds can be moved many times (primary dispersal, secondary dispersal) and by multiple animals prior to seed death or seed germination (Van der Wall and Longland 2004). In this section we will summarize the activities of animal seed dispersers that have been studied in the Caribbean lowland forests of Costa Rica: ants, fish, birds, volant mammals, and terrestrial mammals.

Numerous species of tropical leaf litter ants act as secondary seed dispersers, removing small seeds from fallen

fruits or from the feces of frugivores and transporting the seeds into nests (Kaspari 1993, Levey and Byrne 1993). Ants can act as seed predators, eating and killing some seeds they encounter, but a portion of seeds taken by ants may be discarded intact and in viable condition within refuse piles (Levey and Byrne 1993, García-Robledo and Kuprewicz 2009). Ants may enhance seed germination success and seedling growth via seed cleaning, scarification, or deposition in a nutrient-rich microhabitat that is favorable for seedling establishment (Horvitz 1981, Passos and Oliveira 2002, García-Robledo and Kuprewicz 2009). Usually ants remove seeds only short distances (a few meters) from parent plants and thus may not be as effective at seed dispersal as animals that deposit seeds farther from the source (Howe and Smallwood 1982).

Lowland rain forests on Costa Rica's Caribbean slope contain high ant diversity (437 species found at the 1,600 ha La Selva; Longino et al. 2002), including many leaf litter-dwelling species that interact with fruits and seeds (Kaspari 1993). In field trials involving arrillate seeds of *Renealmia alpinia*, García-Robledo and Kuprewicz (2009) observed that at least four species of leaf-litter ants removed seeds up to 1.8 m from the source. In this study, *Ectatomma ruidum* removed seeds rapidly from sources and enhanced the germination of seeds brought into nests. Ants of the genus *Pheidole*, commonly found throughout forests in the Caribbean lowlands, readily remove and cache *Miconia nervosa* and *M. centrodesma* seeds in refuse piles, having both positive and negative effects on seed survival (Levey and Byrne 1993). Small seeds from the genus *Miconia* appear particularly attractive to leaf-litter granivorous ants with at least 22 species from the tribes Attini, Ectatommini, Ochetomyrmicini, Pheidolini, and Solenopsidini noted removing *M. affinis* seeds from feces of frugivores (Kaspari 1993). Seeds of many *Calathea* species found throughout the Caribbean lowlands possess eliasomes that attract ant seed dispersers including ants from the genera *Odontomachus*, *Pachycondyla*, *Ectatomma*, and *Aphaenogaster* (Le Corff and Horvitz 1995 and references therein).

Frugivory by fish is an understudied realm of seed dispersal biology on the Caribbean slope of Costa Rica. Seed dispersal by fish has been more extensively studied in the flooded forests of central Amazonia where many tree species have buoyant, hydrochorous seeds (Kubitzki and Ziburski 1994 and references therein). Seed dispersal by fish may contribute to distribution patterns of riparian species. Studies of *Brycon guatemalensis*, an abundant frugivorous fish found in the rivers throughout La Selva Biological Station, have found that this species acts as a major disperser of *Ficus insipida* and *F. glabrata* seeds (Banack et al. 2002). *Brycon guatemalensis* consume copious amounts of *Ficus*

seeds and contribute to the upstream dispersal and establishment of this riparian tree species (Horn 1997).

Most Neotropical bird species are, to some extent, frugivorous and may serve as effective seed dispersers for a variety of plant species. Avian frugivores can remove many fruits while foraging and usually defecate or regurgitate intact seeds long distances from source plants (Howe 1977, Levey 1987). Seed deposition within bird feces may enhance seed germination or subsequent removal by secondary seed dispersers (e.g., ants, rodents) (Levey and Byrne 1993). Frugivory and seed dispersal by birds in the Caribbean region of Costa Rica have been critically reviewed by Levey et al. (1994)—therefore, we focus here on studies conducted after the publication of the Levey et al. (1994) review.

The Caribbean lowland region of Costa Rica is especially speciose with regard to birds, containing at least 411 species of which 256 breed in the region (Levey and Stiles 1994). This area contains one of the highest diversities of birds in Central America (also, see previous sections in this chapter). Some lowland forest frugivorous birds feed exclusively on fruits (e.g., *Corapipo altera*, *Euphonia gouldi*, *Manacus candei*, *Pipra mentalis*) while others consume fruits to supplement insectivorous diets (Blake et al. 1990). Many resident avian species recorded in La Selva consume fruits and seeds and over 60% of altitudinal migrants are frugivores that track seasonal fruit abundances (Levey and Stiles 1994).

Loiselle and Blake (1999) evaluated the seed dispersal effectiveness of six frugivorous birds that are common in the region: *Mionectes oleagineus*, *Pipra mentalis*, *Corapipo leucorrhoea*, *Hylocichla mustelina*, *Chlorothraupis carmioli*, and *Euphonia gouldi*. Bird species differed in their reliabilities as consumers of fruits from four species of Melastomataceae and seed deposition patterns differed by bird and plant species. Overall seed dispersal effectiveness can differ widely, even among fruit-eating bird species with high dietary overlap. A study involving seed dispersal agents in plantations and abandoned pastures in the region found that birds are among the most important seed dispersers in plantation habitats, potentially accelerating forest succession (Zamora and Montagnini 2007). Forests of differing ages contain floristic differences that may also affect frugivory and seed dispersal by birds. Overall sugar concentrations of fruits found in secondary lowland forests are higher than those of fruits in primary forests, which results in faster fruit removal rates by birds in secondary habitats, although proportions of fruit removal do not differ among forests (Lumpkin and Boyle 2009).

Though less studied in the Caribbean lowlands, large frugivorous birds such as toucans and aracarís (family Ramphastidae) consume high quantities of fruits and disperse

both large and small seeds over long distances via endozoochory. Though usually found in the forest canopy, *Pteroglossus torquatus*, *Ramphastos sulfuratus*, and *R. swainsonii* have been observed consuming fruits and seeds of the ginger *Renalmia alpinia* in the understory (García-Robledo and Kuprewicz 2009). Toucans may also play an integral role in the dispersal and establishment of some large-seeded palms commonly found in the Costa Rican lowlands (e.g., *Iriartea deltoidea*). Mixed parentage aggregations of *I. deltoidea* seedlings located beneath adult trees are governed by the seed handling behaviors and movement patterns of these large ramphastids (toucans) (Sezen et al. 2009).

Seed dispersal by bats has received much attention in the Neotropics with many studies conducted in the Caribbean lowland forests of Costa Rica. Bats can disperse small seeds (e.g., *Ficus* spp., *Cecropia* spp.) via endozoochory, whereas they disperse large seeds (e.g., *Dipteryx panamensis*, palm seeds) by dropping them during flight or under feeding sites and roosts (Fleming and Heithaus 1981, Kelm et al. 2008, and references therein). Bats may be highly effective seed dispersers owing to their capability for long distance seed dispersal among various habitats (Heithaus and Fleming 1978).

Most phyllostomid bats found in Caribbean lowland forests are highly frugivorous. *Artibeus*, *Carollia*, and *Dermanura* consume fruits and seeds from many understory and canopy plants in the region (Levey et al. 1994). *Artibeus jamaicensis* and *Dermanura watsoni* have been evaluated as highly effective dispersers of seeds from the fig *Ficus insipida* (Banack et al. 2002). Within the Sarapiquí Basin of the Caribbean slope, Melo et al. (2009) found 46 species of large (>8 mm) seeds beneath leaf tents constructed by *D. watsoni*. Their findings had implications on seed and seedling distributions near bat tents within forested habitats—seed densities and seedling abundances were higher under bat tents than in areas away from tents (Melo et al. 2009). Bats, owing to their abilities to forage, feed, and roost in diverse habitats, may serve as effective natural reforestation agents. Artificial roosts constructed throughout a forest–pasture mosaic in the Caribbean lowlands successfully recruited 10 species of bats, including five frugivores/nectarivores (Kelm et al. 2008). These bats transported many seeds from early-successional plants into degraded lands, potentially leading to forest succession within these pasturelands (Kelm et al. 2008). However, further evaluations of seed germination success and seedling growth are needed to evaluate the effectiveness of bats as reforestation agents (Holl 2008).

Seed dispersal and frugivory by terrestrial mammals is a common phenomenon in the forests of the Costa Rican Caribbean slope. Numerous terrestrial species are known fruit-eaters, including agoutis (*Dasyprocta punctata*), collared peccaries (*Pecari tajacu*), armadillos (*Dasyurus novemcinc-*

tus), coatis (*Nasua narica*), tayras (*Eira barbara*), kinkajous (*Potos flavus*), pacas (*Cuniculus paca*), and numerous species of opossums. Most Carnivora likely also consume fruits and seeds to supplement their diets, though their effectiveness as seed dispersers is virtually unknown in this region. Small rodents, particularly the heteromyid rodent *Heteromys desmarestianus*, consume and cache small and large seeds, potentially serving as effective seed dispersers for some plants (especially palms) (Fleming 1974). Many terrestrial rodents consume and destroy seeds while foraging, acting as significant seed predators and only incidental seed dispersers (Smythe 1986).

The seeds of the palm *Socratea exorrhiza* that fall to the forest floor are rapidly encountered by small (*H. desmarestianus*, *Proechimys semispinosus*) and mid-sized (*D. punctata*) terrestrial mammals (Kuprewicz 2010, 2013). Predation of seeds by terrestrial mammals tracks fruiting patterns, with lower predation levels during peak fruit set compared to higher levels at the end of the fruiting season (Notman and Villegas 2005). Seed caching, however, does not appear to follow these fruiting patterns (Notman and Villegas 2005), and hoarding events by agoutis at La Selva are relatively rare (Kuprewicz 2010, 2013).

In forests protected from human hunting in the Caribbean lowlands (such as La Selva), local populations of collared peccaries have recently increased, likely due to direct effects (fewer peccaries killed by hunters than previously) as well as indirect effects (release from predators [large felids] that remain uncommon in the area despite reduced human hunting). Collared peccaries forage singly or in small groups (Romero et al. 2013) and are seed predators that consume and kill many large seeds (e.g., *Dipteryx panamensis*, *Iriartea deltoidea*, *Mucuna holtonii*, *Socratea exorrhiza*) (Kuprewicz and García-Robledo 2010, Kuprewicz 2010, 2013). Peccaries may disperse some seeds via endozoochory or expectoration (Beck 2005), but in the Caribbean forest of La Selva, they act primarily as seed predators; this behavior negatively affects seedling recruitment and may have dramatic implications for future tree distributions and plant propagation (Kuprewicz 2010, 2013). A comparison of seed removal and seed fates in two Caribbean lowland forests (Tirimina Rain Forest Center, a hunted forest, and La Selva, a forest protected from hunting) found that some seed species (*Carapa nicaraguensis*, *Lecythis ampla*, *Pentaclethra macroloba*) had higher seed removal rates in La Selva when compared to Tirimbina. Overall seed dispersal was also higher at La Selva than at Tirimbina (Guariguata et al. 2000). Removal of large terrestrial frugivorous mammals through hunting can have complex effects on the seed dispersal, seed survival, and resultant seedling demography in defaunated regions (Wright et al. 2000).

People and Nature

Human Populations and Demography

As indicated earlier, precontact indigenous populations were substantial but not nearly the size of Maya, Aztec, and Inca populations to the north and south. The Caribbean lowlands constitute part of the Costa Rican archaeological subregion identified as Atlantic Highlands and Watershed. The best-known archaeological site in this area is the Las Mercedes site, uncovered by the railroad construction of Minor C. Keith in the 1870s, and currently located on the campus of EARTH University in Guápiles. Keith removed more than 15,000 items and distributed them among several museums in the United States. In the 1890s the Swedish archaeologist Carl V. Hartman also worked at Las Mercedes and sent many valuable objects to Sweden. This site is dated at about 1,000–2,000 years old and therefore does not provide insight into the earliest indigenous populations (Snarskis 1976). Many additional archaeologically valuable locations are scattered around the Caribbean lowlands, some of them currently under excavation and others undiscovered or untouched.

The human population of Costa Rica's Caribbean lowlands grew slowly throughout the colonial period after the demographic collapse of the indigenous populations (Augelli 1987). Spanish settlers tended to establish themselves in the Central Valley (Palmer and Molina 2004). The Caribbean coast is known during these years for the exploits of a few colorful English and Dutch pirates—the Nicaraguan Caribbean town of Bluefields, for instance, is named after the Dutch pirate Abraham Blauvelt—and not for any substantial settlements of colonists or indigenous people (Ross and Capelli 2003). After Costa Rica's independence from Spain in 1821, the Central Valley population centers (San José, Cartago, Alajuela, Heredia) continued to expand—a trend that was enhanced as coffee production became the dominant economic force in the country. The entire human population of Costa Rica is estimated to have been about 19,000 people in 1770, then 52,000 in 1801, then 200,000 in 1900, then 875,000 in 1950 (Augelli 1987). Sixty years later Costa Rica's population size had been multiplied by a factor of five, reaching a total of 4,564,000 inhabitants (Centro Centroamericano de Población 2011).

Significant populations of Europeans and North Americans did not arrive in the Caribbean lowlands until the construction of the railroad between Alajuela and the Caribbean coast in the late nineteenth century. The railroad was built to transport coffee, Costa Rica's major agricultural export crop, from the central highlands (where it was grown) to the Caribbean port of Limón for export to Europe. The builder and financier of this railroad, US investor Minor C.

Keith, started the Caribbean lowland banana industry to help finance the railroad project. Excellent, extensive treatments of both the coffee and the banana industries of Costa Rica are recommended (Chapman 2007, Chomsky 1996, Koeppl 2008, Paige 1997, Palmer and Molina 2004, Ross and Capelli 2003). West Indian Afro-Caribbean workers were brought to the Costa Rican lowlands to work on the railroad and on the banana plantations. By 1883 there were 902 Jamaicans in Limón Province, and by 1927 there were 18,003. These workers were not granted Costa Rican citizenship until 1948, and they were not allowed to leave Limón Province, even to work on the Pacific banana plantations. Today about one-third of the population of Limón Province is made up of West Indian immigrants and their descendants (Biesanz et al. 1987). The distinctive language and culture of the Limón area are due to the influence of these Afro-Caribbean workers and their descendants.

As mentioned previously, Puerto Limón is the largest city in the Caribbean lowlands. Although it is the second largest city in Costa Rica, its population of 63,000 puts it at a distant second to the capital of San José with its population of about 335,000. Other Caribbean-side population centers include Guápiles (~19,000), Siquirres (~18,000), Guácimo (~7,000), and Puerto Viejo de Sarapiquí (~6,000). Human settlement in the Caribbean lowlands increased dramatically during the 1960s, 1970s, 1980s, and 1990s owing to at least three factors: Costa Rica's extremely high birth rate before 1960 (Coale 1983), a deliberate governmental policy to move people from the Central Valley to the “hinterlands,” and farm labor immigration from other Central American countries (particularly from Nicaragua). The birthrate has fallen in recent years (Coale 1983) but the Caribbean lowlands continue to see increasing populations.

Agriculture and Pesticides

The Caribbean lowland area of Costa Rica is threatened by the same dangers that affect other tropical systems—deforestation, loss of biodiversity, genetic fragmentation of plant and animal populations, spread of alien invasive species, climate change, human population increase, and the pressure to value short-term economic gains over long-term sustainability. Some of these subjects are treated in other sections of this chapter. Here we focus on one particular theme, that of agricultural development and pesticide use, because it is a topic that is critically important in its own right and also because it brings many of these other areas into clear focus. A consideration of agriculture and pesticide use is also intimately related to emerging issues such as valuation of ecosystem services, global food security, poverty alleviation, the objectives of the Millennium Eco-

system Assessment, and the new Sustainable Development Goals (SDGs).

Globally, the use of pesticides (insecticides, fungicides, rodenticides, herbicides, and germicides) has increased dramatically in the past seventy years (Carvalho 2006) and every corner of the planet, including Arctic ice, bears traces of these chemicals (Chernyak et al. 1996, Cone 2006, Pelley 2006). Much early use of insecticides was related to mosquito/malaria control (Jaga and Dharmani 2003, Lubick 2007), but a significant proportion of pesticide application has now been turned toward agricultural food production (Monge et al. 2005, Wesseling et al. 1999). Although the use of pesticides has certainly led to increased food production—the so-called Green Revolution—(Cooper and Dobson 2007), some of these positive effects are being lost through evolving resistance to the chemicals by pests and non-target organisms (Brausch and Smith 2009, Jansen et al. 2011, Nolte 2011, Raymond et al. 2001) or offset by various direct and indirect calculated costs of pesticide use. Pesticides have been shown to have serious human health consequences, both acute (Soares and Porto 2009) and chronic (Abhilash and Singh 2009, Charboneau and Koger 2008, Nag and Raikwar 2011, Yearout et al. 2008), as well as a range of environmental impacts including soil and water contamination (Liess and von der Ohe 2005) and non-target organism toxicity (Berny 2007, Kendall and Smith 2003, Pisani et al. 2008). The role of pesticides in the endocrine and developmental disruption of wildlife and humans (see Buchanan et al. 2009, Casals-Casas and Desvegne 2011, Mnif et al. 2011, Soim and Smagghe 2007 for reviews) is also becoming an increasingly powerful concern.

Both the negative and positive aspects of global agricultural development and pesticide use are seen in microcosm with the specific case of the Caribbean lowlands of Costa Rica over the past several decades. DDT was used widely and heavily in Costa Rica from 1957 to 1985 (to the tune of 1,387 total tons during that period) to control mosquito-borne malaria (Pérez-Maldonado et al. 2010, Duszeln 1991). Today DDT and other banned organochloride pesticides (OCPs)—widely known as persistent organic pollutants (POPs)—have a relatively low and uniform distribution in soils across the country (Daly et al. 2007a) but, as recently as 2009, levels of DDT in soil and children's blood serum were considered above acceptable levels in two rural communities in the Limón area (Pérez-Maldonado et al. 2010). Pesticide use in Central America doubled between 1980 and 2000 (Wesseling et al. 2005). During the 1990s, Costa Rica's annual use of 4 kg of pesticides per inhabitant and 38 kg per agricultural worker was the highest in all of Central America (Wesseling et al. 2001). In recent years, Costa Rica has been at the top of the world's coun-

tries in pesticide use (Polidoro et al. 2008, World Resources Institute 2007), on the basis of the number of kg of active ingredients applied annually to each hectare of agricultural land (52 kg a.i. [active ingredients]/ha/yr in 2000). Raw pesticide import data from 1977 to 2009 have been analyzed for Costa Rica (de la Cruz et al. 2014) and indicate increases in the variety of chemicals used, as well as their environmental hazards. Pesticides are used on large volume agricultural crops such as banana, coffee, pineapple, rice, and heart-of-palm (also called palm heart), as well as on non-traditional agricultural export crops (NTAEs) such as plantain, carrot, cassava, squash, and cut flowers. Pesticides are applied to crops for export as well as for local (within Costa Rica) consumption.

A third to a half of Costa Rica's imported pesticides are used in banana production (Castillo et al. 2006) and most of Costa Rica's banana production today is in the Caribbean lowlands. Bananas are the world's number one fruit consumed and in the past few years Costa Rica has been among the world's top three banana-exporting countries, along with Ecuador and the Philippines (Barraza et al. 2011). In 2009 Costa Rica's banana plantations covered more than 50,000 hectares and employed 35,000 workers (CORBANA 2009). The effects of chemicals used by the United Fruit Company in Costa Rica during the sigatoka (*Mycosphaerella musicola*) fungus outbreak of the 1930s led to an extended workers' strike (Marquardt 2002). Decades later, the claims of worker sterility from the use of the nematicide DBCP (marketed under the name Nemagon) led to several class-action lawsuits settled out of court or in favor of the plaintiffs (Ling and Jarocki 2003). DBCP has been linked to several types of cancer among Costa Rica's banana workers (Wesseling et al. 1996).

Chlorothalonil is a pesticide currently in use on Costa Rican banana plantations, with application rates of up to 45 times per year (Chaves et al. 2007). This fungicide is considered to be highly toxic to humans (Caux et al. 1996, Margni et al. 2002, Sherrard et al. 2003) and in Costa Rica has also been shown to be toxic to fish, birds, and aquatic invertebrates (Castillo et al. 2000). Fortunately, unlike DDT, it breaks down rapidly in Costa Rica's tropical climate (45% degradation after 24 hrs), but some residues are still present after 85 days and toxic metabolites are also persistent (Chaves et al. 2007). In Costa Rica, as has been the case elsewhere, the pesticide industry has changed from using a few broadly acting chemicals to using a wide range of active ingredients with shorter active lives (Galt 2008a).

Chemicals from agricultural production find their way into the soils and rivers of the Caribbean lowlands. Sediments from clearing land for plantations also drain into the area's rivers and modify habitat for local freshwater organ-

isms and for more distant marine organisms. The streams receiving water from Caribbean lowland banana-processing plants are home to altered macroinvertebrate communities in the presence of pesticide levels that are well below those responsible for acute toxicity (Castillo et al. 2006). A more distant effect is produced by the Río Estrella, which drains a large area of banana plantations and discharges into the Caribbean Sea 10 km north of Parque Nacional Cahuita and the offshore coral reef (Roder et al. 2009). Aerosolized pesticides are carried from their lowland sites of application to higher elevations on the slopes of Volcán Barva, where they precipitate out over “pristine” mid-elevation forests (Daly et al. 2007b).

Cassava growers in an indigenous Bribri community near Limón indicated that they had had no training in use of agricultural chemicals and that less than one-third of them used protective clothing during spraying (Polidoro et al. 2008). In this same community, Bribri women who worked with chemically sprayed plantains reported more respiratory problems than women who did not work in agriculture (Fieten et al. 2009).

In the face of worrisome data regarding pesticide effects, there is potentially some good news. The most toxic chemicals used in Costa Rican agriculture do have less toxic alternatives (Humbert et al. 2007). An organic treatment for the post-harvest control of banana crown rot has been developed by scientists at EARTH University (Demerutis et al. 2008). Some international banana companies have sought Rainforest Alliance certification, which lends the required stamp of “sustainability” to products sold to segments of the European market. In Costa Rica, education and extension services also effectively reduce the intensity of pesticide use (Galt 2007). For example, on a potato farm near Cartago pesticide use was reduced if there were minors (children) in the household or if the farmer had taken an agricultural course (Galt 2008b).

Recent studies indicate that the current standards for pesticide residues in the destination countries are creating pressure for less pesticide use in the producing countries, including Costa Rica (Galt 2008c). Consumer groups around the world indicate a “willingness to pay” more for bread and produce in exchange for less pesticide use (Batte et al. 2007, Boccaletti and Nardella 2000, Chalak et al. 2008, Florax et al. 2005, Foster and Maurato 2000, Kahn 2009). Adherence to “developed country pesticide standards” in developing countries (Okello and Swinton 2010) is one powerful way to break the ominous “circle of poison” of the recent past whereby chemicals banned in developed nations were sold and used in the Third World, only to return to the developed world as residue on imports (Weir and Shapiro 1981). In a study of pesticide use on five vegetables

(carrot, chayote, corn, green bean, and squash) grown in Costa Rica both for national use and for export, pesticide use was less on the produce bound for export to the United States (Galt 2008), reportedly because of EPA guidelines on pesticide residues.

Although large-scale completely pesticide-free agriculture is probably not possible, it is entirely possible to imagine a scenario that combines the following: (1) economic incentives for the use of chemicals with lower toxicity and with lower application rates, (2) development of more organically grown and free-trade products, (3) industrial, academic, and extension training to maximize worker knowledge and safety, (4) continued and intensified consumer pressure for healthy products, (5) enforced guidelines on pesticide residues in consumer nations, (6) environmental monitoring of air, soil, and water by government and the scientific community, (7) epidemiological studies on the relation between disease and exposure to chemicals, and (8) creative high technology solutions to food security such as removing pesticides from fruit juices in the final stages of processing. Many of these efforts are currently underway, albeit not universally, in the Caribbean lowlands of Costa Rica. Costa Rica is in a position to attempt a unified approach to intensified but non-destructive agriculture because of its long history of agricultural activity, its world-recognized conservation efforts, and the well-established multi-institutional and international scientific research being conducted within the country.

Conservation

The conservation history of Costa Rica since the 1950s has been well documented and analyzed. Excellent treatments are available regarding the founding of the national park and reserve system (Boza 1993, Evans 1999, Wallace 1992), the proliferation of conservation efforts during the past 60+ years (Calvo-Alvarado 1990, Campbell 2002a, Johnson and Clisby 2009, Powell et al. 2000), and the establishment of specific projects and private reserves (Butterfield 1994, Chornook and Guindon 2008, Nadkarni and Wheelwright 2000, Wheelwright and Nadkarni 2014). Case studies of Costa Rican conservation initiatives such as payment for environmental services (Dick et al. 2010, Morse et al. 2009, Pagiola 2008, Sánchez-Azofeifa et al. 2007, Sierra and Russman 2006, Snider et al. 2003), the Mesoamerican Biological Corridor (Dettman 2006, Sader et al. 2004), the Biodiversity Law of 1998 (Miller 2011), participatory resource management (Sims and Sinclair 2008), and carbon sequestration (Lansing 2011) are also available.

For many decades Costa Rica has been held up as an example to the world for the amount of its land under pro-

tection, its sustainable ecotourism, and the strong environmental ethic among its citizens. Critics and scholars have pointed out some of the discrepancies between this image and stark reality, including illegal logging and harvesting of forest products, underfunding of national parks, negative tourism impacts on protected areas, duplicated or disorganized conservation efforts, and unequal distribution of the economic benefits of conservation initiatives (Campbell 2002a,b, Hoffman 2011, Silva 2003, Sylvester and Avalos 2009, Vivanco 2006). Several unquestionable conservation success stories do exist, however, as does a continuing willingness on the part of interested parties to invent new strategies to cope with problems that arise. The title of an article by one of the founders of Costa Rica's National Park system, Mario A. Boza, remains as apt today as it was upon its publication—with regard to environmental solutions, “Costa Rica is a laboratory, not Ecotopia” (Boza et al. 1995).

More than a dozen national parks, wildlife refuges, and biological corridors have been created in the Caribbean lowlands since 1970, when the Tortuguero area was first protected and then made into a National Park in 1975 (for a map of the region's protected areas, see Fig. 16.2). As a heuristic exercise, we have chosen to compare the Tortuguero area to the San Juan–La Selva (SJLS) Biological Corridor because of several fascinating similarities and instructive differences in the establishment and current operations of these two areas. Among the similarities in the scenario for the creation of these two entities are (1) the realization that an iconic vertebrate species was about to be lost, (2) rapid legal action to protect the nesting areas of these animals, (3) cooperation among scientists, government officials, and representatives of non-governmental organizations (NGOs) to create and consolidate the protected areas, (4) the large size and ecological diversity of the area under protection, (5) the welcome outcome—a conservation success story—at least in terms of halting the precipitous decline of the iconic vertebrate species, and (6) increasing pressure on the protected areas from other sources in recent years. Notable differences in the two stories are (1) the dominant conservation paradigms at the time of establishment of the protected areas, (2) the funding and management of the areas, (3) the ownership of the land contained within the protected areas, (4) the extent of community income from ecotourism, and (5) the strength of international scientific research conducted in the protected areas.

The 35 km stretch of the Caribbean coast between the Tortuguero and Parismina rivers has probably been a nesting ground for the Atlantic population of the green turtle *Chelonia mydas* and other sea turtles for many hundreds if not thousands of years (Spotila 2004). Early Spanish explor-

ers noted the vast turtle populations in this area and named the zone “Tortuguero” (place of turtles) (Ross and Capelli 2003). Indigenous people and colonial settlers harvested eggs and adult turtles for local consumption and for export (Jackson 1997, Lefever 1992), but large-scale exportation of eggs, meat, and calipee in the mid-twentieth century dramatically increased the pressure on the Costa Rican green turtle population almost to the point of extinction. Dr. Archie Carr, a turtle specialist from the University of Florida, had been monitoring these animals since 1955 and became alarmed at their rapid decline in the early 1970s (Carr 1967, Carr et al. 1978). He spoke urgently with people in the international conservation community and the Costa Rican government and prompted a series of actions over the next several years. First, an executive decree was issued in 1970, prohibiting the harvesting of turtles and their eggs along the beach and protecting a portion of the nesting area. The 19,000 ha Parque Nacional Tortuguero was established as one of the first of Costa Rica's national parks by Law 5680 in 1975, during the presidency of Daniel Oduber. A contiguous area of 92,000 ha was established in 1985 as the Refugio Nacional de Vida Silvestre Barra del Colorado. In 1994, a 50 ha parcel of land wedged between the two protected areas became the Dr. Archie Carr Wildlife Refuge and the site of the John H. Phipps Biological Station. Two marine turtle laws, 7906 (1999) and 8325 (2002), banned catching the turtles at sea.

Owing to these conservation efforts, Tortuguero now has the largest group of nesting green turtles in the entire Atlantic population (see also Cortés, chapter 17 of this volume). From 1971 to 2003, there was a 417% increase in the number of nests, with estimates of 104,000 nests per year and 17,000–37,000 nesting females per year during the 1999–2003 period (Troëng and Rankin 2005). A very active international research effort, including a graduate program based at the University of Florida (supported by the Phipps Biological Station in Costa Rica), has contributed important information on the Tortuguero green turtles, including data on genetic diversity of nesting females (Bjornald et al. 2005), spatial distribution of nests (Tiwari et al. 2005), adult survival (Troëng and Chaloupka 2007), effect of sea surface temperatures on nesting (Solow et al. 2002), hatchling success (Tiwari et al. 2006), levels of bacteria in nests (Santoro et al. 2006), and the genetic composition of juvenile foraging groups (Monzón-Argüello et al. 2010).

The green turtle is still considered to be endangered over its entire range (Rieser 2012, Seminoff and Wallace 2012), although some populations are in better shape than others (Broderick et al. 2006, Seminoff and Shanker 2008). The Tortuguero population, although rebounded, is still nowhere near the levels estimated for Precolombian pop-

ulations (Jackson 1997, McClenachan et al. 2006, Troëng and Rankin 2005). These turtles take nearly 30 years to reach sexual maturity (Frazer and Ladner 1986) and the overharvesting of juveniles in the open ocean (both intentionally and as bycatch of commercial fishing and shrimping operations) could lead to reduced numbers of mature adults available for breeding in the future (Lahanas et al. 1998, Lagueux 1998, Mortimer 1995). Despite these caveats, the population of green turtles at Tortuguero in recent years appears healthy (Chaloupka et al. 2008). The hope persists that the Tortuguero/Barra del Colorado protected area will also benefit other threatened and endangered vertebrates such as manatees (Smethurst and Nietschmann 1999), hawksbill turtles (Bjorndal et al. 1993, Troëng et al. 2005), and leatherback turtles (Troëng et al. 2007), but the recovery of these species seems less optimistic.

Since its inception, the scientific research in the Tortuguero protected area has been combined with ecotourism and revenue generation for the local community (Meletis 2007, Lee and Snepenger 1992). Turtle watching tourism has increased greatly over the years, as have the revenues generated by ecotourism (Ballantyne et al. 2009, Jacobson and Figueroa Lopez 1994). A training program for local tourist guides was developed (Jacobson and Robles 1992) and turtle watching guidelines for sustainable ecotourism have been suggested (Landry and Taggart 2010). Every year scores of volunteers arrive to patrol the beach during the laying season (Campbell and Smith 2006), in order to tag adults, count nests, and watch over hatchlings. The basic tourism package has changed over the years from a “hard” (rugged) to a “soft” (more comfortable) experience (Harrison and Meletis 2010, Place 1991). With tourism has come a certain amount of disturbance for the human community as well as for the turtles (Harrison and Meletis 2010, Jacobson and Figueroa López 1994), such as waste management problems, trampling of beaches, and light from houses distracting hatchlings during their migration to the sea. Adjustments to the tourism offerings are made periodically in an adaptive management paradigm (Meletis and Campbell 2009, Harrison and Meletis 2010). Many segments of society are involved in the turtle conservation enterprise, including scientists, local guides, tourists, volunteers, citizen scientists, donors, funding agencies, government officials, and tourism-dependent business people. Tortuguero turtle conservation has drawn the attention of social scientists nearly to the extent that it has attracted the attention of biologists (Campbell 2002b).

Twenty years after the establishment of Parque Nacional Tortuguero, a parallel scenario arose in the Caribbean lowland forest along the Río San Juan with the great green macaws (*Ara ambiguus*). Where once there had existed

large flocks of these birds in Costa Rica’s Caribbean lowland feeding and nesting areas, their numbers were reduced to about 50 breeding pairs by the early 1990s (Monge et al. 2003). Other populations still existed in reproductively isolated groups from Honduras to Ecuador but the total species population was down to around 5,000 individuals when the species was designated as CITES I, critically endangered in 1985 (Müller 2000) and was then reduced further to about 3,700 individuals over the next ten years (Monge et al. 2009). The decline of this macaw in Costa Rica appeared to be due more to habitat destruction than to direct harvesting of the animals, although illegal collecting of eggs and hatchlings for the pet trade was documented. Land-clearing for cattle pastures and banana plantations resulted in a loss of 80% of suitable habitat for these birds by the 1990s (see Deforestation section, this chapter). Of particular concern was the logging of *Dipteryx panamensis* trees, a critical food and nesting tree for the great green macaw in Costa Rica (Stiles and Skutch 1989). Because of its extremely dense wood, this tree had been virtually immune to logging pressures until the introduction of a particularly strong carbon steel chainsaw blade. George V.N. Powell, a noted ornithologist who had been working in Monteverde with highland birds, was also working in the Caribbean lowlands with the great green macaw population. He sounded the alarm about the macaws (Powell et al. 1999) in much the same manner that Archie Carr had done with the green turtles at Tortuguero.

Starting in the early 1990s, there was much talk of biological corridors as a conservation strategy (Beier and Noss 1998, Newcomer 2002, Sánchez-Azofeifa et al. 2003). The concept of a Paseo Pantera (Path of the Panther), connecting protected areas from Mexico to Colombia, had been proposed by Archie Carr III (son of the Archie Carr who promoted the creation of Parque Nacional Tortuguero) and other scientists from the Wildlife Conservation Society (WCS) and the Caribbean Conservation Corporation (CCC), along with USAID and other funding agencies (Kaiser 2001). The GEF (Global Environmental Facility) was established in 1991 with World Bank funds to support conservation initiatives (Cléménçon 2006, Ervine 2007, 2010, Griffiths 2004), including the Mesoamerican Biological Corridor (MBC; a reformulated version of the Paseo Pantera) (Miller et al. 2001, Minc et al. 2001). This concept was formalized in 1992 at the UN Conference on Environment and Development (UNCED) in Río de Janeiro (MBC 2002). In 1997, an official treaty to create the MBC was signed by Central American countries, with Mexico joining later. Each country was tasked with developing its own plans—Costa Rica chose to create a series of smaller corridors, each administered by a user group with the involvement of at



Fig. 16.8 Entrance to the Boca Tapada community in the Refugio Nacional Vida Silvestre Maquenque at the northern end of the San Juan–La Selva Biological Corridor. The community lies along the Río San Carlos near the confluence with the Río San Juan and the border with Nicaragua. This area is the breeding and nesting area of Costa Rica's remaining population of Great Green Macaws.

Photo by Deedra McClearn.

least one representative from MINAE (Ministerio de Ambiente y Energía). The treaty version of the MBC now had two principal aims: physical connectivity of protected areas and sustainable economic development in the communities around the protected areas (Finley-Brook 2007).

To return to the plight of the great green macaw, the San Juan–La Selva Biological Corridor (246,608 ha) was defined in 1997, as part of the larger national corridor initiative and also to protect the nesting area of the great green macaw. This is a mixed-use corridor, with private lands and agricultural fields. The northern portion of the corridor was set aside as the Refugio Nacional de Vida Silvestre Maquenque in 2005 after it became clear that the political will and the financing did not exist to make this a fully protected national park. The refuge is contiguous with the Nicaraguan Indio Maíz national park across the Río San Juan, and is the only remaining nesting area of the great green macaw in Costa Rica. The *Dipteryx panamensis* trees were protected

from logging throughout the entire country in 2008 by executive decree. The management of the SJLS Corridor is handled through the Tropical Science Center (TSC) by Olivier Chassot (who had been a research assistant working for George Powell in 1994) and Guiselle Monge. The establishment of Maquenque and the SJLS Corridor can be considered a conservation success story in the sense that the decline of this population of macaws seems to have been arrested and their numbers may even be increasing after 15 years of protection. There is a modest biological field station at the Lagarto Lodge in Boca Tapada (on the edge of the Maquenque wildlife refuge) (Fig. 16.8) which hosts groups of Costa Rican and international students. Small-scale efforts to combine conservation and ecotourism have met with some success, but revenues from ecotourism have not radically transformed the local economy, which remains based in agriculture, particularly pineapples and yucca (Jackiewicz 2006). Ironically, the sort of development that

the SJLS corridor communities are expecting and demanding is exactly the sort of development that has caused social and environmental problems in Tortuguero.

The publications pertaining to the SJLS Corridor, the Refugio Nacional de Vida Silvestre Maquenque, and the Costa Rican portions of the MBC include technical reports from governments and from NGOs (Lampman 2000, Sader et al. 2004), as well as popular articles about the great green macaw (Chassot and Monge 2002, Chassot et al. 2005, 2009, Monge et al. 2005). The scientific literature contains a number of analyses of land use, notably those employing remote sensing (satellite and airplane overflight imagery) to assess forest coverage, forest biomass, and the distribution of particular tree species (Chun 2008, Kalacska et al. 2008, Wang et al. 2008).

Every park, wildlife refuge, and private reserve has its unique story, just as every conservation program has its champions and its critics (Fig. 16.9). Parque Nacional Tortuguero was created during the time of the early park system, just after the “closing of the frontier” in the 1960s (Augelli 1987). The SJLS Corridor came into being twenty years later, during an era with a much larger Costa Rican human population, no more freely available, government-sponsored land for small-holder farming, and the expectation of economic benefits from any and all biological conservation projects. A transfrontier mixed-use biological corridor is a very different beast from a discrete national park. After 20 years of existence and billions of dollars spent on the MBC, the GEF has drawn its share of criticism regarding the practical implementation of conservation programs and the neoliberal agenda that it represents (Cléménçon 2006, Ervine 2007, 2010). Nonetheless, at a smaller spatial scale the SJLS Corridor and the Refugio Nacional de Vida Silvestre Maquenque can be credited with protecting critical habitat. The maintenance of forest cover in these areas will have a lasting impact on the conservation of Costa Rica’s biodiversity. The first fifteen years represent a promising start towards the optimal scenario that biodiversity conservationists envision, but agricultural pressure and a local sense of unfulfilled economic expectations pose formidable risks to this vision.

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Fig. 16.9 These images of Costa Rican wildlife stamps from the 1980s depict the green turtle and the great green macaw, and represent an increasing environmental awareness by both the Costa Rican government and the public in general.

Perspectives on the Future

We began this chapter with the theme of geography but quickly added the theme of time—the deep time of the geological perspective as well as the short time frame of such human enterprises as road building and forest clearing. The coauthors are scientists and conservationists and all are aware of the importance of spatial and temporal scale in our research activities. We also recognize that our own efforts are often limited in both space and time, but that the maintenance of intact ecosystems in today’s world requires planning and implementation activities that are temporally prolonged and spatially extensive. The rapidity of the transformation of the Costa Rican Caribbean lowlands has been astonishing. We wonder whether there is common ground for an ecologist, a hotel owner in Maquenque, a turtle-tagging volunteer at Tortuguero, a local subsistence farmer, a NASA remote sensing expert, a MINAE park ranger, a Bribri landowner with a homegarden and a field of cassava, and a corporate responsibility executive at a banana company all to work together to ensure that ecosystem services and biodiversity are maintained in the long run. We certainly believe there are common ground and a common cause that will trigger our joint attention to address these issues successfully in an integrated manner in the near future.

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